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Kaneohe Bay Sewage Diversion Experiment: Perspectives on Ecosystem Responses to Nutritional Perturbation[1]

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ABSTRACT: Kaneohe Bay, Hawaii, received increasing amounts of sewage from the 1950s through 1977. Most sewage was diverted from the bay in 1977 and early 1978. This investigation, begun in January 1976 and continued through August 1979, described the bay over that period, with particular reference to the responses of the ecosystem to sewage diversion.

The sewage was a nutritional subsidy. All of the inorganic nitrogen and most of the inorganic phosphorus introduced into the ecosystem were taken up biologically before being advected from the bay. The major uptake was by phytoplankton, and the internal water-column cycle between dissolved nutrients, phytoplankton, zooplankton, microheterotrophs, and detritus supported a rate of productivity far exceeding the rate of nutrient loading.

These water-column particles were partly washed out of the ecosystem and partly sedimented and became available to the benthos. The primary benthic response to nutrient loading was a large buildup of detritivorous heterotrophic biomass. Cycling of nutrients among heterotrophs, autotrophs, detritus, and inorganic nutrients was important.

With sewage diversion, the biomass of both plankton and benthos decreased rapidly. Benthic biological composition has not yet returned to presewage conditions, partly because some key organisms are long-lived and partly because the bay substratum has been perturbed by both the sewage and other human influences.

MAN SEEKS TO PRESERVE, protect, and manage natural ecosystems in the face of increasing human pressure. Rational use of the environment implies that there exists adequate basis to predict the consequences of human activities with some confidence. All too often, the observational and experimental data base is inadequate for predictions about total ecosystems, although we may be able to foresee consequences of some human actions on selected components of the system.

Direct manipulations for the purpose of performing experiments on ecosystems are ordinarily limited to relatively small or simple ecosystems (Nelson and Edmondson 1955; Schindler 1974, 1977). By contrast, predictable and quantifiable technological events can provide opportunity to apply experimental methods to ecosystem analysis on a scale of complexity, cost, and size not ordinarily available to environmental scientists. One identifies events that are likely to be quantitatively significant, and then manipulates those events as total-ecosystem experiments. Such experiments should be designed to highlight and understand the environmental responses as an integrated whole rather than simply to monitor legally or socially mandated or accepted variables that may have little significance in deciphering total ecosystem function.

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Deliberate total-ecosystem experiments have the potential to provide information that might be ambiguous or unavailable from nonmanipulative observations of the system. In treating a technological event as an experiment, the environmental scientist's "manipulation" is conceptual rather than actual. The manipulation is imposed by the technological event. Perhaps the best-known total-ecosystem experiment manipulating such an event is the study of the response of Lake Washington to sewage diversion (Edmondson 1977; Edmondson and Lehman 1981).

In a well-chosen total-ecosystem experiment, the technological event being monitored is likely to have effects that are large in comparison with the described, but uncontrolled, variability of the system from other causes. Questions are based on theories of ecosystem structure and function; conformance between theoretical expectations about ecosystem responses to the manipulation and realized results may provide validation and quantification of those theories in complex, "real-world," yet well-described settings. Lack of conformance provides a basis to alter old theories or develop new ones. In either case, results enable one to develop appropriate environmental management strategies.

Manipulations involving significant reductions in the degree of ecosystem stress are likely to be more socially acceptable than those involving significant increases. If ecosystems do not gain or lose major ecologically significant components in the process of a changing stress regime, then it should be equally informative to examine increasing or decreasing stress, since either change represents an ecosystem perturbation. One assumes, and indeed hopes for the sake of the environment, that ecosystem responses to perturbations are reversible within some limits. If this assumption is generally valid, then one learns something about the extent to which environments are modified by controlled application of a specific perturbation and the degree of environmental resilience to such perturbations.

The Kaneohe Bay Sewage Diversion Experiment tested the following hypothesis:

> Effects of domestic sewage discharged into this subtropical coastal marine ecosystem are reversible; consequently, the ecosystem may be returned to presewage conditions by the diversion of that sewage.

So stated, the hypothesis was primarily of political interest, and made Kaneohe Bay the subject of intense local public debate. The hypothesis can be restated in a form of more general interest to environmental researchers and managers:

> Domestic sewage discharged into ecosystems exerts influence by modifying the biomass and foodweb characteristics of those systems. Hence, ecosystem responses to sewage and its diversion can be ascertained from a comprehensive description of nutrients added to the system, storage and cycling within the system, and flushing from the system.

It is inevitable that an ecosystem would respond to a large alteration of the degree of nutritional subsidy, but we did not know how useful material cycling would be in assessing ecosystem response. Consequently, this investigation largely tested the utility, rather than the validity, of our hypothesis.

Kaneohe Bay, Hawaii, has been a very appropriate ecosystem for a total-ecosystem experiment. The bay, its boundaries, and inputs to it are relatively well described; there exists a large body of information from which to begin the experimental analysis. Coconut Island (also known as Moku O Loe), in the southeastern portion of the bay, has been the site of a University of Hawaii marine laboratory (now part of the Hawaii Institute of Marine Biology) since 1951. Many environmental observations, including several extensive investigations, have been made by University of Hawaii personnel and visiting investigators. The Naval Ocean Systems Center and its predecessors have had facilities at Mokapu Peninsula, on the southeastern border of the bay, since 1967 and have engaged in environmental studies in the bay. In 1970 the Congress of the United States mandated that the U.S. Army Corps of Engineers undertake a planning study of Kaneohe Bay and its environs; that mandate has resulted in several useful

studies. This general background of information provided valuable resources for the total-ecosystem experiment we have performed.

The data base for this investigation includes available current and historical environmental information from various published and unpublished sources. It is inevitable that comprehensive total-ecosystem analyses rely on information that might not be readily available to readers outside the state of Hawaii. We also collected a large amount of biological and chemical data ourselves. Details of our sampling and analysis procedures are presented in the Appendix.

This study has considered the bay over the past two decades, with particular emphasis on an experimental period between January 1976 and August 1979. The period emphasized spans a sewage-diversion episode, which occurred as two steps in December 1977 and May 1978. This diversion is the experimental manipulation; fluctuations of other environmental variables are uncontrolled elements of the experiment. This report highlights effects on the ecosystem attributable to the sewage discharge and to its diversion.

One might expect various results from sewage input and its diversion: (1) The sewage might contain significant amounts of directly toxic materials or toxic byproducts from pesticides, herbicides, chlorine, or heavy metals. (2) High biochemical oxygen demand (BOD) from the sewage, possibly coupled with hydrogen sulfide generation, might impose toxic effects. (3) In contrast to these inhibitory effects, materials in the sewage might have a primarily nutritional effect on the biological community.

Available information for the bay suggested that the most conspicuous effects of the sewage were in terms of increased biomass and productivity, together with altered community structure. Available evidence suggested that even near the sewer outfalls, no major taxa had been totally eliminated although the structure of benthic communities had been dramatically altered. Much of the observed taxonomic alteration of the ecosystem apparently represented effects of biotic "kills" from freshwater runoff and siltation, combined with biotic succession responding to altered nutritional status from the sewage. We therefore assumed that the major role of the sewage was nutritional modification rather than intoxication. We developed our analysis of the ecosystem, its responses to the sewage, and its responses to the diversion of sewage around the concept that the sewage represented an identifiable perturbation at the base of the foodweb. The varying balance of the mass of nutrients in the Kaneohe Bay ecosystem is the central theme of this study.

Despite this focusing theme, we could not consider sewage to the exclusion of other environmental variables acting on an ecosystem subject to the vagaries of nature. The Kaneohe Bay Sewage Diversion Experiment may be considered controlled in comparison with many field studies, but is messy in comparison with experiments that might be conducted in a beaker or incubation chamber. The experiment gained realism at the expense of laboratory simplicity.

The study serves as a model for at least one approach to comprehensive analysis of an ecosystem. As is true for any model, this one has weaknesses that will be explicitly stated or implicitly obvious. A major weakness, which is destined to plague studies of this sort until funding agencies more generally accept the need for long-term knowledge of ecosystem variation, is the short timespan of our data record. Some variables in the ecosystem simply did not reach equilibrium with the postdiversion nutrient status of the bay within the timespan of our investigation. Moreover, postdiversion environmental fluctuation unassociated with sewage did not replicate prediversion conditions. While it will be possible to return to the bay a decade hence in order to examine equilibrium conditions, the course of return and the influences of variables other than sewage on that course will have been lost. It would have been desirable to have a longer record of both prediversion and postdiversion conditions in the bay.

Another weakness of this study is a consequence of the considerable biological com-

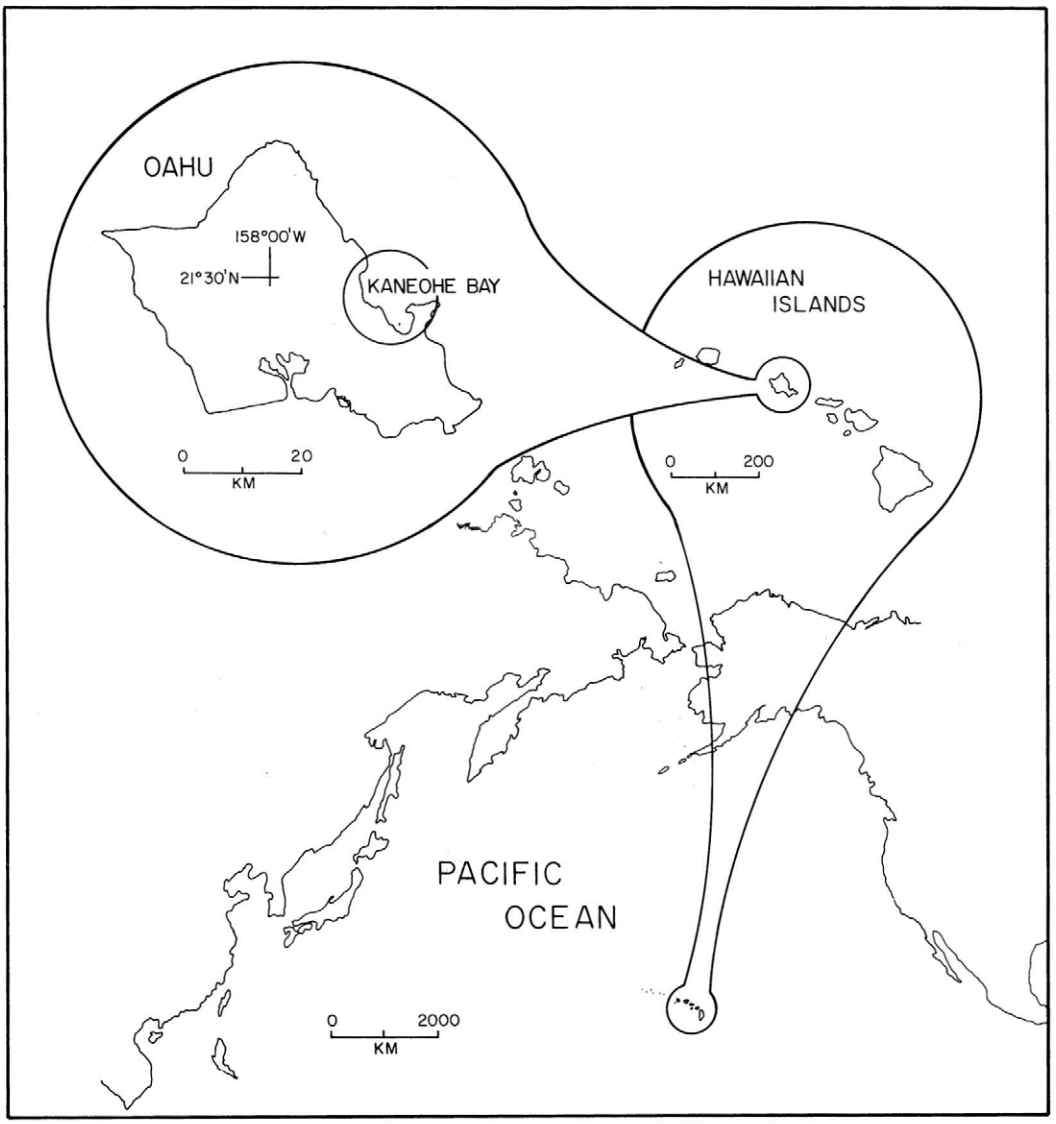


FIGURE 1. Kaneohe Bay in global perspective.

plexity of many tropical nearshore ecosystems. Because it was impractical to sort large numbers of samples to great taxonomic detail, we emphasized biomass rather than biological composition. The biomass information proved to be quite useful; the limited community composition data proved useful in qualitative terms. While it would be desirable to combine more compositional detail with good biomass data, we remain unsure that such an effort is both statistically and economically feasible in a high-diversity system like Kaneohe Bay and other coral reefs. In the meantime, quantitative assessment of biomass and largely qualitative compositional assessment appear a feasible and useful compromise.

In summary, the investigation presented here had four primary objectives:

1. To analyze the responses of a par-

ticular ecosystem to sewage discharge and to the diversion of that discharge, with the discharge, diversion, and ecosystem responses being considered as a deliberate experiment.

2. To provide, as an example to be followed and improved upon, a description of environmentally significant characteristics in an aquatic ecosystem. Toward this end, we have taken some pains in this presentation to state and reiterate the interconnections among those characteristics of the bay.

3. To compile and to consider data relevant to Kaneohe Bay in specific and to the island of Oahu in general, to be used for future environmental studies in Hawaii.

4. By serving each of the above purposes, to advance our knowledge of ecosystem description, analysis, and management.

This paper is organized somewhat unconventionally because the study on which it is based was comprehensive. We have put the methods in an appendix to maintain the flow of the text. In the text, we first describe the general environmental setting of the ecosystem, using anecdotal and historical information and very little of our own data. Building on this foundation, in the next section we describe the results of numerous measurements made during our study of water chemistry and biomass variables, including their responses to sewage diversion. In a further section, we discuss those data in terms of metabolic activity, and describe several additional experiments on dynamic responses of the ecosystem. We construct a simple mass balance model of nitrogen and phosphorus in the southern basin, and estimate uptake and release of nitrogen and phosphorus by phytoplankton, zooplankton, and soft- and hard-bottom communities. In the final section, we evaluate our research program and offer some guidelines for similar research.

GENERAL ENVIRONMENTAL SETTING

Kaneohe Bay is a semienclosed embayment on the northeast coast of Oahu, Hawaii (Figure 1). The landward boundary of the Kaneohe watershed is sharply delineated by a nearly vertical mountain range (Figures 2 and 3); the seaward boundary of the bay is a barrier reef that extends across the bay mouth (Figures 2 and 3).

The bay includes components of both estuary and coral reef, two quite different kinds of ecosystem. Coral reefs develop best in an environment free of terrestrial influence. Kaneohe Bay is a weakly developed estuary and thus has moderate land influences in the form of freshwater, sediment, and nutrients. However, even these small influences can be damaging to reef development.

The interplay between these contrasting environments can perhaps best be appreciated by means of a simplified northeast to southwest physiographic cross section of the bay (Figures 3 and 4). Consider this cross section from the ocean, through the outer and inner portions of the bay, to the land at the bay margin. The letters *A* through *I* denote first occurrence of successive physiographic zones, with letters being repeated for largely redundant zones.

A is the windward reef slope, beyond the oceanic margin of the bay. There is no significant estuarine influence on the water or the sea floor. Reef organisms, particularly corals, able to withstand large oceanic swells grow on a limestone pavement which remains from an earlier reef-construction episode in the history of the bay. Sediments of this region are calcareous sand and rubble. The sea floor climbs gently from the top of a cliff in water about 20 m deep, 6 km offshore, to the surf zone in water about 2 m deep and about 4 km offshore, marking the outer portion of the bay.

B is the algal reef flat, a zone 1–2 km wide and 1–2 m deep. It is predominantly a hard-bottom area with abundant corals, algae, and other reef organisms. The energy of ocean waves is absorbed in this zone, protecting the reefs in the lagoon and producing a landward flow of water. The algal flat and upper reef slope are highly productive, in terms of both organic material and calcareous sedimentary material. The landward

FIGURE 2. Oblique air photograph facing northwestward up the long axis of Kaneohe Bay. The photo illustrates the steep mountains that mark the watershed boundary. The high degree of urban development along the southwestern shoreline of the bay is apparent in the foreground, and the Kaneohe Municipal Sewage Treatment Plant can be seen in the lower center portion of the photograph. (Photograph property of the R. M. Towill Corp.)

flow of water across the algal flat redistributes the organic and inorganic products of these zones.

The *B* zone gives way to a sand-dominated backreef flat, zone *C*, also 1–2 km wide. The sand, produced by biological and wave erosion of calcareous material in zones *A* and *B*, is carried into zone *C* by wave-driven currents. The resulting sand wedge is growing landward, with the inner margin marked by an exposed sand bar.

The cross section described to this point would fit any Oahu windward fringing reef. Because this reef does not abut the shoreline, the prograding backreef sand flat terminates in a lagoonward depositional slope (*D*). Some algae and seagrass are found on the upper portion of the slope and on the edge of the flat itself. Sediments of this region are rich with organic detritus from both local production and debris that has drifted in from the algal flat. This steeply sloping de-

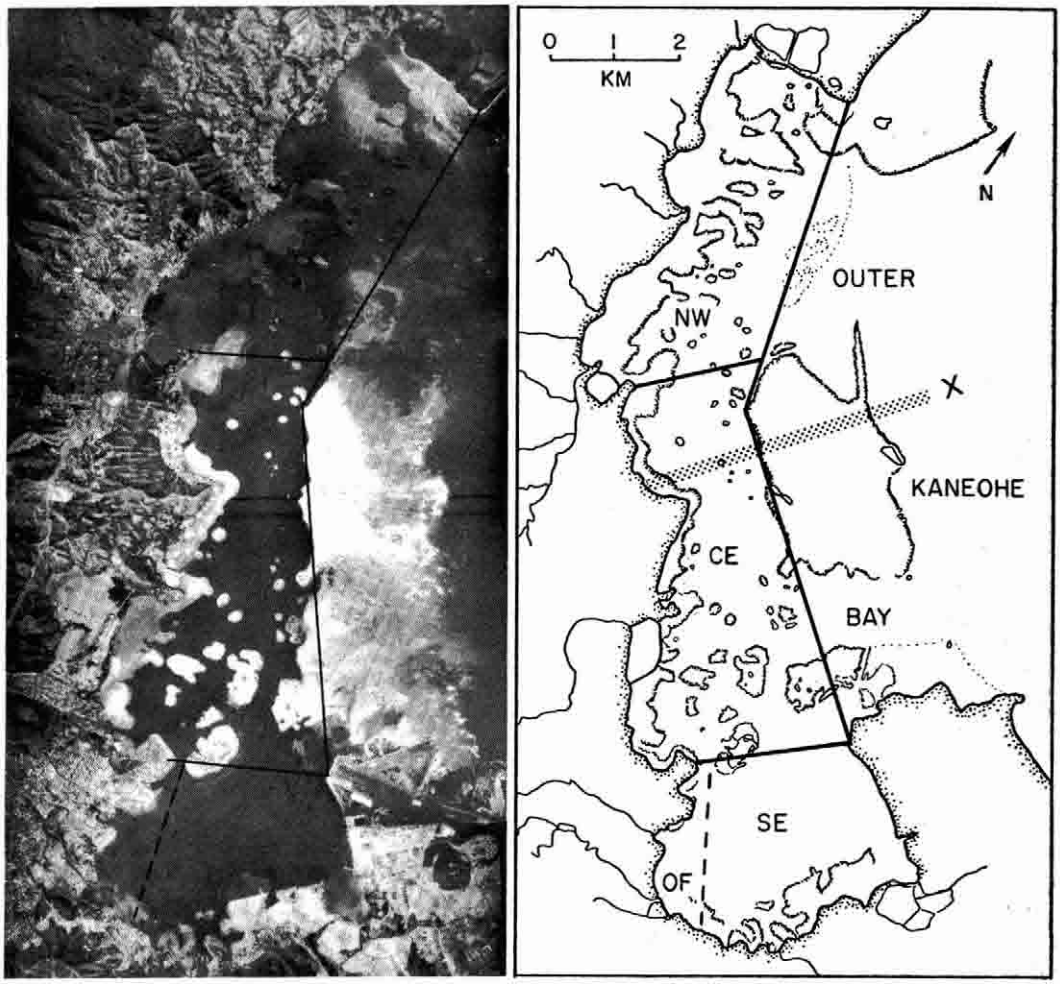


FIGURE 3. Vertical air photograph of Kaneohe Bay (courtesy of the Naval Undersea Center) and map of the bay showing sectors and cross section (X) discussed in text.

positional face extends to the lagoon floor (zone E) at 15 m depth.

Leaving the cross section briefly, let us consider another significant feature of the outer bay barrier reef. The shallow reef flat is breached at its northwest and southeast ends by channels that connect the ocean and the lagoon (Figure 3). The northern channel is presently the deeper of the two, since a shallow reef across it was dredged to a depth of approximately 15 m in the 1930s, and serves as the main channel for the minor shipping activity in the bay. The southern channel has a natural sill depth of approximately 10 m. Both channels affect water circulation in Kaneohe Bay.

Returning to the cross section, zones B–D are here termed Outer Kaneohe Bay and suffer little influence from land. The remainder of the bay is known as Inner Kaneohe Bay. The lagoon (zone E) is uniformly about 15–17 m deep and floored throughout by mud with numerous quiet-water reefs (zones F–H).

The proportion of noncalcareous material in the lagoon sediments (largely clay minerals from basalt) increases with proximity to shore. This gradient is more clearly de-

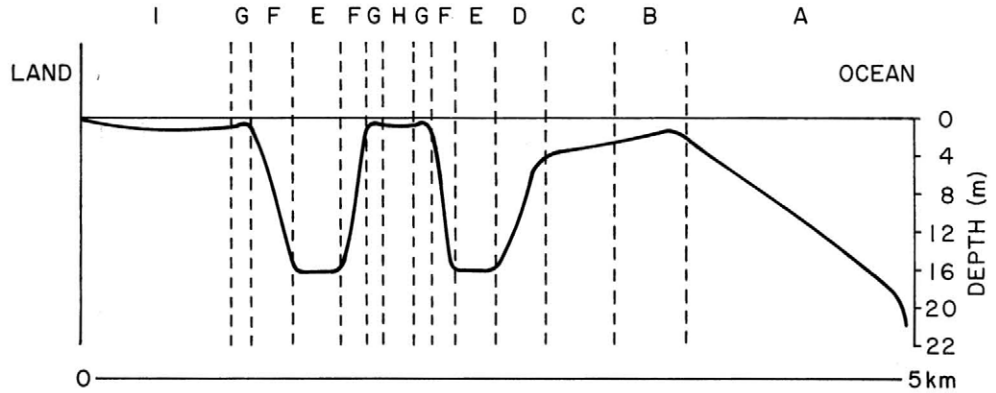


FIGURE 4. Generalized cross section of Kaneohe Bay. The location of the section is shown on Figure 3, and the zones denoted by the letters are discussed in the text. The horizontal dimension is given for general orientation, although the figure is not to scale horizontally.

fined in the central sector of the bay, which has few streams, than at either end of the bay, where major streams are located.

The lagoon waters support a relatively high standing crop of phytoplankton and zooplankton. There are abundant midwater fishes, ranging from planktivores to top carnivores (sharks), and the fish population is locally significant to commercial, subsistence, and sport fishing. Biota of the lagoon floor are sparse.

Within the lagoon are two major types of quiet-water coral reefs—patch reefs and fringing reefs. Both have steep reef slopes (*F*) that rise from the lagoon floor to near sea level. These slopes have supported the highest coral cover of any portion of Kaneohe Bay, and indeed among the highest coral cover to be found in the Hawaiian Islands. The abundance and diversity of reef fish tend to be high on these slopes. Fine mud similar to that of the lagoon floor fills spaces around corals. Within the central portion of the bay (near the cross section), the reef slopes have been substantially modified by the growth of large amounts of a green alga (*Dictyosphaeria cavernosa*). The alga has altered the biological structure of the slopes, including covering and killing most of the coral on some reefs. In the southeastern portion of the bay the reef-slope corals are largely dead, and the slopes are now covered by a variety of detritus-feeding organisms (sponges, barnacles, tunicates, oysters, etc.).

Some patch reefs have been dredged to depths of 3–5 m, and the dredged areas tend to have a fauna similar to the slopes. A prominent exception is that dredged areas in the southern portion of the bay tend to have a somewhat higher coral cover than nearby undredged reef slopes.

The reef slope gives way to a well-defined, hard-bottom reef crest (*G*), which is particularly well developed in the central portion of the bay. The crest is a wave-resistant algal ridge like the crests of many open-ocean reefs. In the southern portion of the bay, the crest has largely degenerated through the activity of various bio-eroding organisms that inhabit the reef rock.

The crest is the highest part of these quiet-water lagoonal reefs, and is slightly exposed by low spring tides. It gives way to a slightly (10–20 cm) deeper reef flat covered by sand and rubble (*H*), with some algae and occasional coral heads. Smaller patch reefs may have only a vestigial reef flat or none at all, being instead a "crest" across the entire reef top.

The fringing reef flat (*I*) has been distinguished from the patch reef flats because of a prominent component of land-derived mud, sand, and rubble. Land-derived mud on the reef flats is particularly conspicuous in the northwestern portion of the bay,

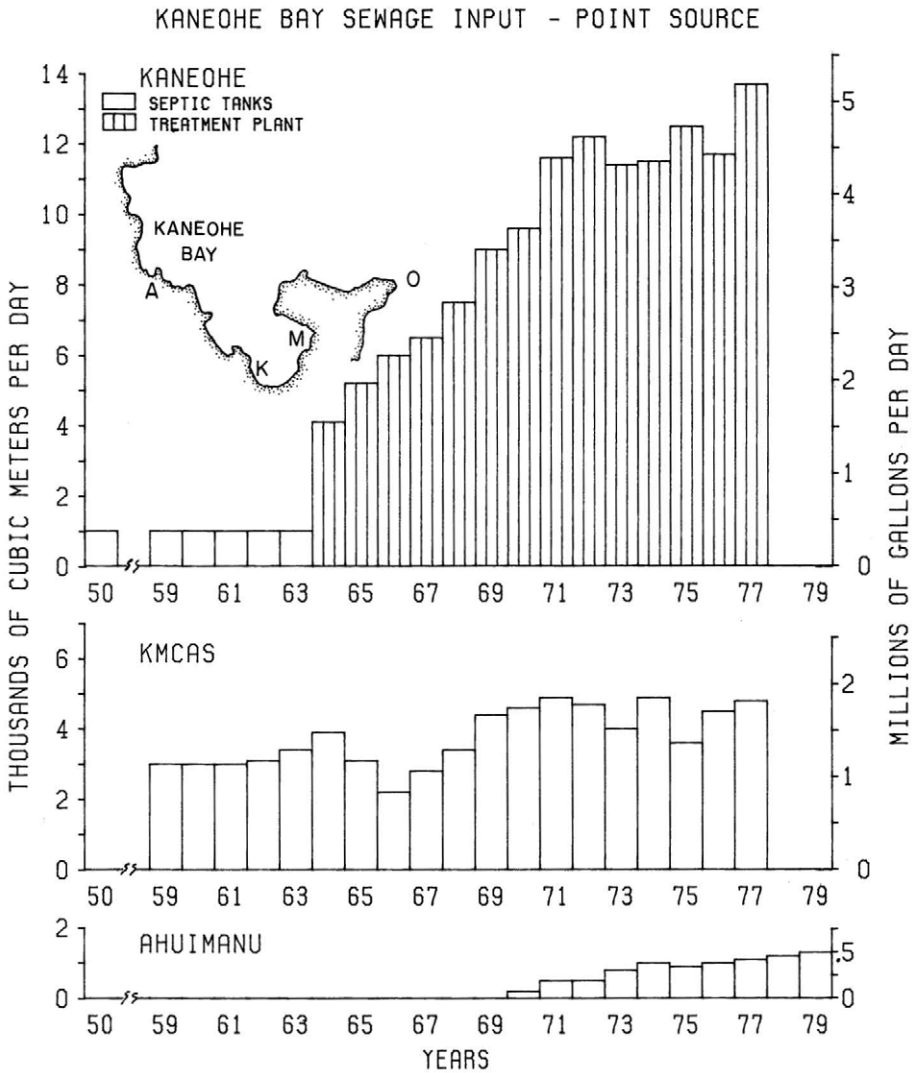


FIGURE 5. Three major point-source discharges of sewage into Kaneohe Bay. Data from City and County of Honolulu. Map (inset) shows the locations of the three bay outfalls (*A*, *K*, *M*) and the new Mokapu ocean outfall (*O*). *A* = Ahuimanu; *K* = Kaneohe; *M* = Kaneohe Marine Corps Air Station (KMCAS).

where the reefs have been highly modified by siltation. The land-derived sand and rubble extends along virtually the entire perimeter of the bay, largely confined to the shoreward portion of the flat. The fringing reef flat in much of the bay has a relatively high standing crop of fleshy algae.

Water over the fringing reef flat, particularly in the southeastern portion of the bay, tends to have a somewhat depressed salinity and to be more turbid than in the open lagoon. Turbidity in the northwestern end of the bay is dominated by inorganic land-derived sediment. The turbidity in the southeastern portion of the bay was produced by organic material most of the time before sewage diversion; whenever heavy rains occur, red land-derived mud colors the water over the fringing reef flat and over much of the lagoon.

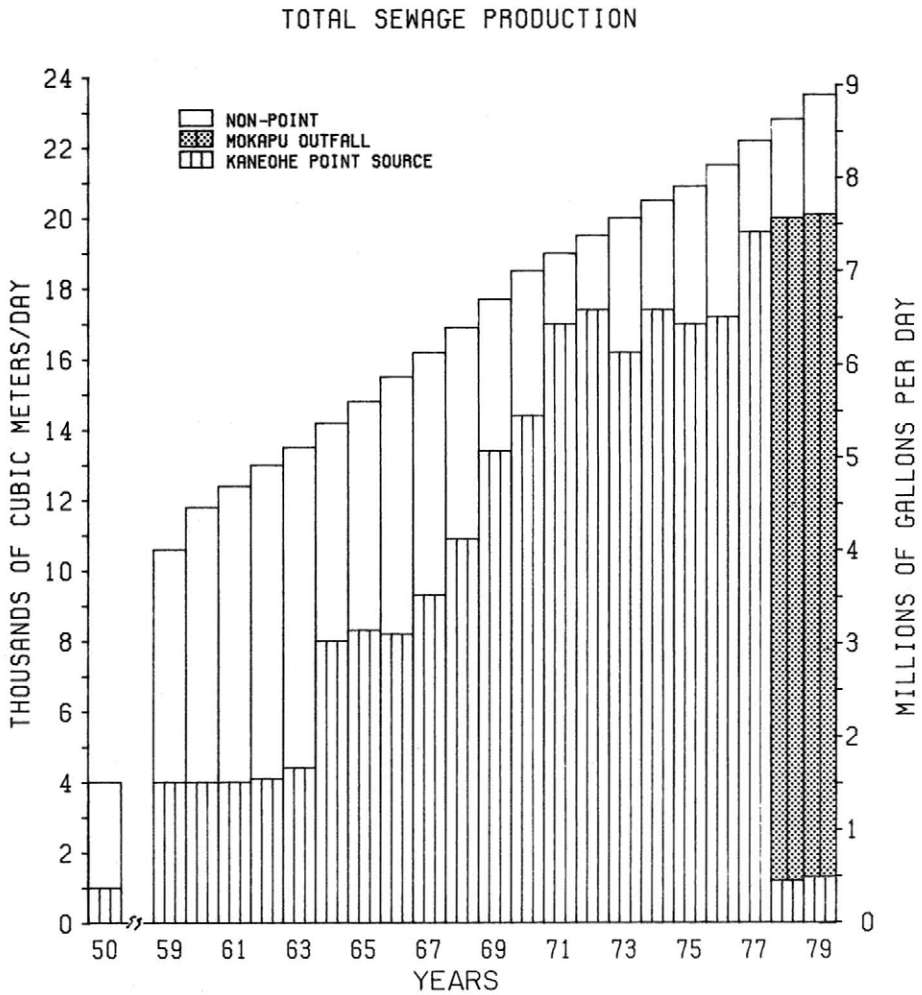


FIGURE 6. Point-source discharge and estimated additional sewage production in the Kaneohe watershed.

Population Growth and Sewage Discharge

The diversion of domestic sewage from Kaneohe Bay is the basis for the experiment described here, and sewage input is intimately tied to human population density. The southern portion of the Kaneohe watershed is, except for central Honolulu, one of the most densely populated areas on the island. The northern two-thirds of the watershed supports a population density below five persons per hectare (DPED 1977).

The history of human population growth in the Kaneohe watershed (Devaney et al. 1976; DPED 1977) shows a steady population of fewer than 5000 persons until 1920, when the numbers began to grow rapidly. The rate of growth was accelerated in 1957 and 1960 by completion of two tunnels connecting Kaneohe with the Honolulu urban center. The 1980 population was 60,000 persons.

Figure 5 illustrates the recent history of sewage discharge into Kaneohe Bay in response to population growth. From 1951 through 1977, the Kaneohe Marine Corps Air Station (KMCAS) discharged a relatively constant sewage load at an outfall in

7 m of water in the southeast corner of the bay. In 1971 the sewage treatment plant was upgraded from primary to secondary treatment (KMCAS STP), and approximately 1000 $m^3 \cdot day^{-1}$ of the effluent was diverted to water a golf course.

Before 1963 the town of Kaneohe was served by private septic tanks and cesspools and by large septic tanks that discharged into a stream entering the southern corner of Kaneohe Bay. Those septic tanks delivered a total discharge of about 1000 $m^3 \cdot day^{-1}$ (C. L. Lau, City and County of Honolulu, Department of Public Works, pers. comm.). In August 1963 a subsecondary (trickling filter) treatment plant (the Kaneohe STP) began operation with an outfall in 8 m water depth in the southern corner of the bay. In 1970 a small secondary sewage treatment plant (Ahuimanu STP) began operation and discharged into a stream flowing into the northwestern portion of the bay.

In 1975 construction of a deep ocean outfall was begun, to divert sewage from the Kaneohe and adjacent Kailua watersheds. During a brief period in November and December 1977 the Kaneohe municipal sewage discharge was shunted back and forth between the bay and the ocean outfall. The Kaneohe sewage was permanently diverted in December 1977, and the Marine Corps sewage was diverted in May 1978. Discharge into the bay continues from the small Ahuimanu STP.

By July 1977 point-source sewage discharge into Kaneohe Bay was approximately 19,400 $m^3 \cdot day^{-1}$: 13,500 $m^3 \cdot day^{-1}$ (70%) at the Kaneohe outfall, 4800 $m^3 \cdot day^{-1}$ (25%) at the Marine Corps outfall, and 1100 $m^3 \cdot day^{-1}$ (5%) at the Ahuimanu outfall. This discharge decreased to 1100 $m^3 \cdot day^{-1}$ upon diversion of the two major sources to the ocean outfall.

Nonpoint-source sewage discharge is difficult to measure. An upper bound can be established from the number of cesspool users in the watershed (about 10,000 in 1978; C. L. Lau, pers. comm.) and the per capita sewage discharge rate. This rate can be calculated from the 1978 population (56,500 persons; DPED 1977) and the 1978 treatment plant discharge rate (Figure 5); the 46,500 persons served by the treatment plant had a per capita daily discharge rate of almost 400 liters. This figure has been combined with the population data to give total watershed sewage production for both point and nonpoint sources (Figure 6). Total sewage production approximately doubled between 1959 and 1977, while point-source discharge increased almost fivefold. The Mokapu deep-ocean outfall has apparently returned the point-source discharge to approximately 1950 levels.

Plots of approximately weekly records for nitrogen and phosphorus concentration and

TABLE 1

COMPOSITION OF KANEOHE SEWAGE EFFLUENT

	moles $\cdot m^{-3}$	g $\cdot m^{-3}$
Nitrogen		
ammonium	0.90	
dissolved organic	0.76	
particulate (estimated from particulate carbon; assume molar C : N $\approx$ 6)	0.2	
Phosphorus		
phosphate	0.17	
dissolved organic	0.04	
particulate (estimated from particulate carbon; assume molar C : P $\approx$ 106)	0.01	
Silicon	0.5	
Suspended solids		38
Particulate carbon estimated as 40% by weight of suspended solids)	1.3	
Biological oxygen demand		32
Residual chlorine		2.0
Trace metals (range)		
aluminum		N.D.–0.25
cadmium		N.D.–0.05
chromium		N.D.–0.006
copper		N.D.–0.02
iron		0.6 –1.05
mercury		N.D.
nickel		N.D.–0.025
lead		N.D.–0.03
zinc		N.D.–0.38

SOURCE NOTE: Data primarily from STP logs; trace metal data from Nomura and Young 1974; silicon data were gathered by our project for the KMCAS effluent.
N.D. = non-detectable.

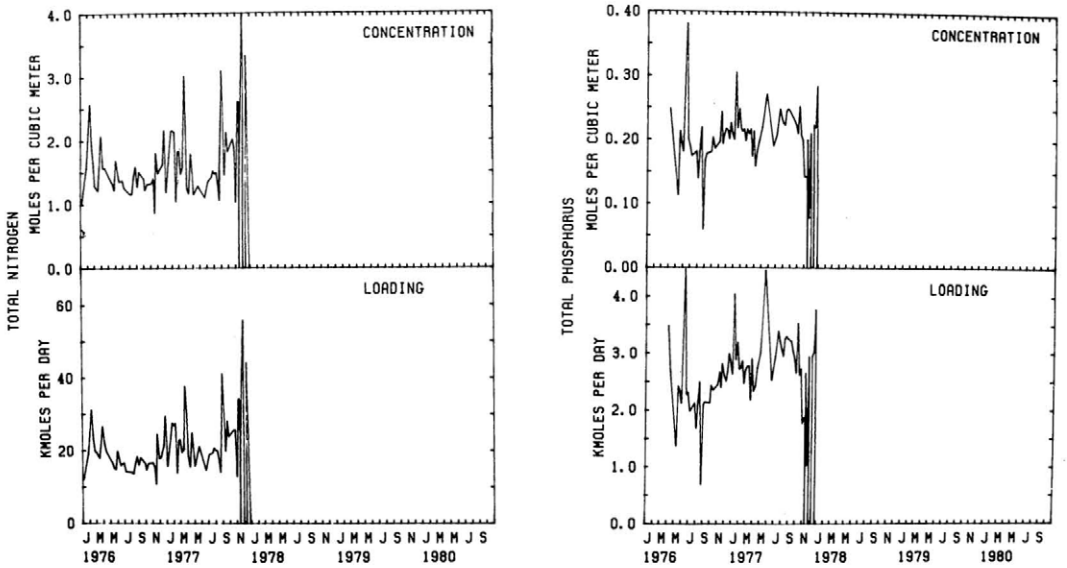


FIGURE 7. Concentration and loading of total nitrogen and phosphorus discharge from the Kaneohe STP during the present investigation. Data from City and County of Honolulu.

loading in the municipal outfall (Figure 7) show the low variability typical of treatment plant output. The few spikes of high loading represent periods of high rainfall and runoff through storm drains into the sewerage system. The oscillation at the end of the record represents the period when discharge was switched between the ocean and the bay.

Table 1 summarizes data on average composition of the Kaneohe STP effluent. Of particular interest are the partitioning of nitrogen and phosphorus between organic and inorganic fractions. About half of the dissolved nitrogen is present as ammonium; the rest is organic nitrogen, which is probably not as readily available to biological utilization as the ammonium. Most (80%) of the phosphorus is phosphate, and the remainder is organic phosphorus.

Dimensions of the Bay and Watershed

The shape of Kaneohe Bay approximates that of a rectangle 13 km long and 4 km wide. The inner portion of the bay (Figure 3), of primary interest to this study, presents a relatively homogenous physiographic setting. It is protected from substantial wave activity and affected by a spatially varying regime of land-derived environmental perturbations. Table 2 summarizes some key dimensions of the inner bay: it has approximately 28 km of shoreline, an area of approximately 31 km^2, and a volume of approximately $266 \times 10^6 m^3$. The water depth (mean $\approx$ 8 m) is bimodally distributed—47 percent of the bay is relatively flat lagoon floor deeper than 10 m, and 33 percent is reef flat or other shoal areas shallower than 1.5 m. The remainder of the bay is composed of generally steep, narrow reef slopes (Figure 8).

It is convenient for many analyses to divide the bay into four sectors (Figure 3). The outfall sector (OF), in the southern corner of the bay, was under the immediate influence of the Kaneohe municipal sewer outfall. That sector is somewhat arbitrarily isolated from the southeast (SE) sector, which received the Marine Corps sewage. These two sectors together make up the "southern basin," and are clearly isolated from both the remainder of the inner bay and the outer bay.

The central (CE) sector lies between the southern basin and the northwest (NW)

TABLE 2

DIMENSIONS OF INNER KANEOHE BAY AND THE KANEOHE WATERSHED

	SHORELINE LENGTH (km)	AREA (km^2) < 1.5 m DEPTH	AREA (km^2) 1.5–10 m DEPTH	AREA (km^2) > 10 m DEPTH	AREA (km^2) TOTAL	MEAN DEPTH (m)	VOLUME ($10^6 m^3$)
Inner Kaneohe Bay							
Southern basin							
OF	3.4	0.29	0.71	0.07	1.07	5.0	5.35
SE	6.8	1.28	1.84	4.18	7.30	10.2	74.24
subtotal	10.2	1.57	2.55	4.25	8.37	9.5	79.59
Transition zone							
CE	8.8	3.40	1.66	7.20	12.26	9.8	119.68
NW	9.0	5.53	1.83	3.48	10.84	6.1	66.41
subtotal	17.8	8.93	3.49	10.68	23.10	8.1	186.09
Inner bay total	28.0	10.50	6.04	14.93	31.47	8.4	265.68

	AREA (km^2) < 5 m ELEVATION	AREA (km^2) 5–250 m ELEVATION	AREA (km^2) > 250 m ELEVATION	AREA (km^2) TOTAL	MEAN ELEVATION (m)
Kaneohe watershed	13.3	65.8	17.9	97.0	180

sector. The central and northwest sectors may be considered a transition zone between outer Kaneohe Bay, which is essentially oceanic in character, and the southern basin.

The watershed adjacent to Kaneohe Bay covers 97 km^2, three times the inner bay area (Table 2). The watershed boundary is well delineated by steep cliffs that rise abruptly from approximately 250 m to a ridgeline with an elevation of up to 800 m (Figure 2). Most of the watershed consists of rolling hills at elevations of 5–250 m.

Meteorology

Meteorological variables exercise major control on processes within any ecosystem. Chief among the significant meteorological controls acting on Kaneohe Bay are rainfall and evaporation, which influence bay salinity and the delivery of dissolved and particulate materials from land; wind, which mixes the bay, influences density stratification, exercises secondary control on mixing through surf activity outside the bay, and affects evaporation; solar radiation, which provides the energy for photosynthesis, thus driving foodweb activity; and air temperature, which affects water temperature, hence biological activity. Meteorological and hydrographic variables collected at stations shown in Figure 9 were analyzed to typify watershed conditions.

Figure 10 shows air temperature, relative humidity, wind speed, rainfall, and evaporation at Coconut Island. All except evaporation are based on continuing, long-term measurements of those variables. Evaporation was calculated from the first three variables listed and water temperature using the formula of Jacobs (1942; discussed by Smith and Jokiel 1978). The calculated evaporation rates are in reasonable agreement with an empirical relationship between rainfall and measured pan evaporation rates (Takasaki, Hiroshima, and Lubke 1969).

Air temperature at Coconut Island shows a seasonal oscillation and averages about 23° C. Relative humidity is rather constant, near 80 percent.

Rainfall in the watershed increases toward the mountains because of orographic lifting of the moist trade-wind air. The gauge data from Coconut Island can be used to rep-

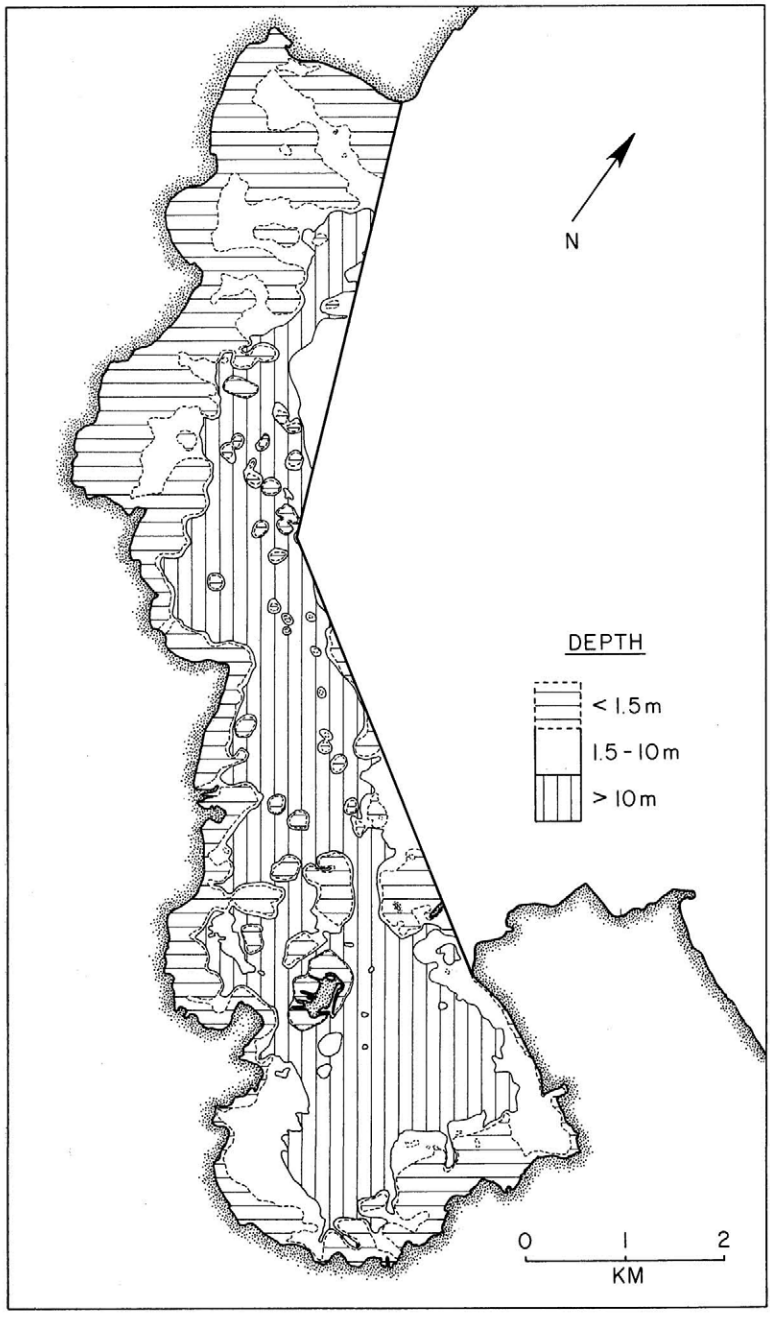


FIGURE 8. Map showing division of inner Kaneohe Bay into three major depth regimes (from Roy 1970).

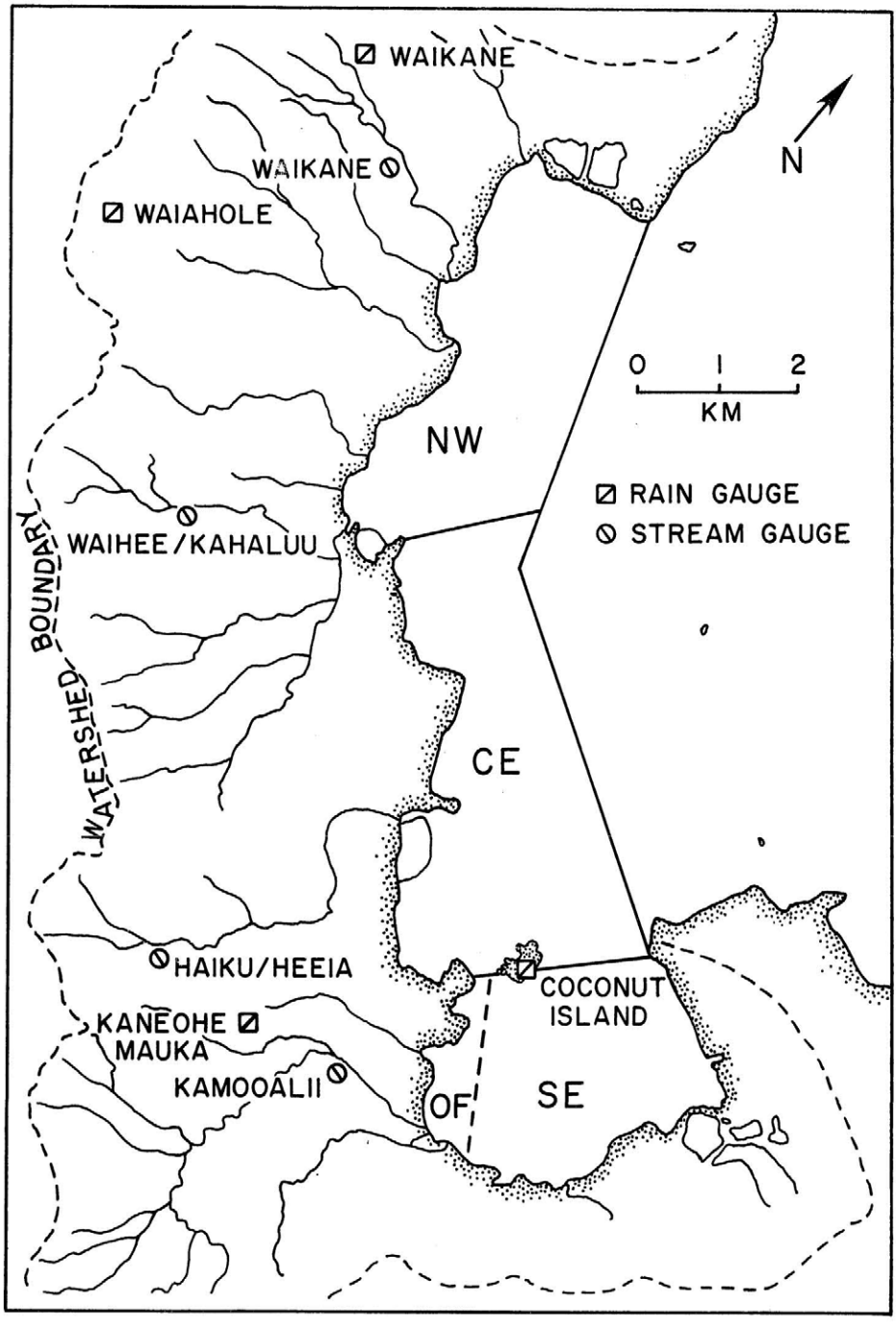


FIGURE 9. Map of Kaneohe Bay, watershed boundary, and stream and rain-gauge stations used in this investigation.

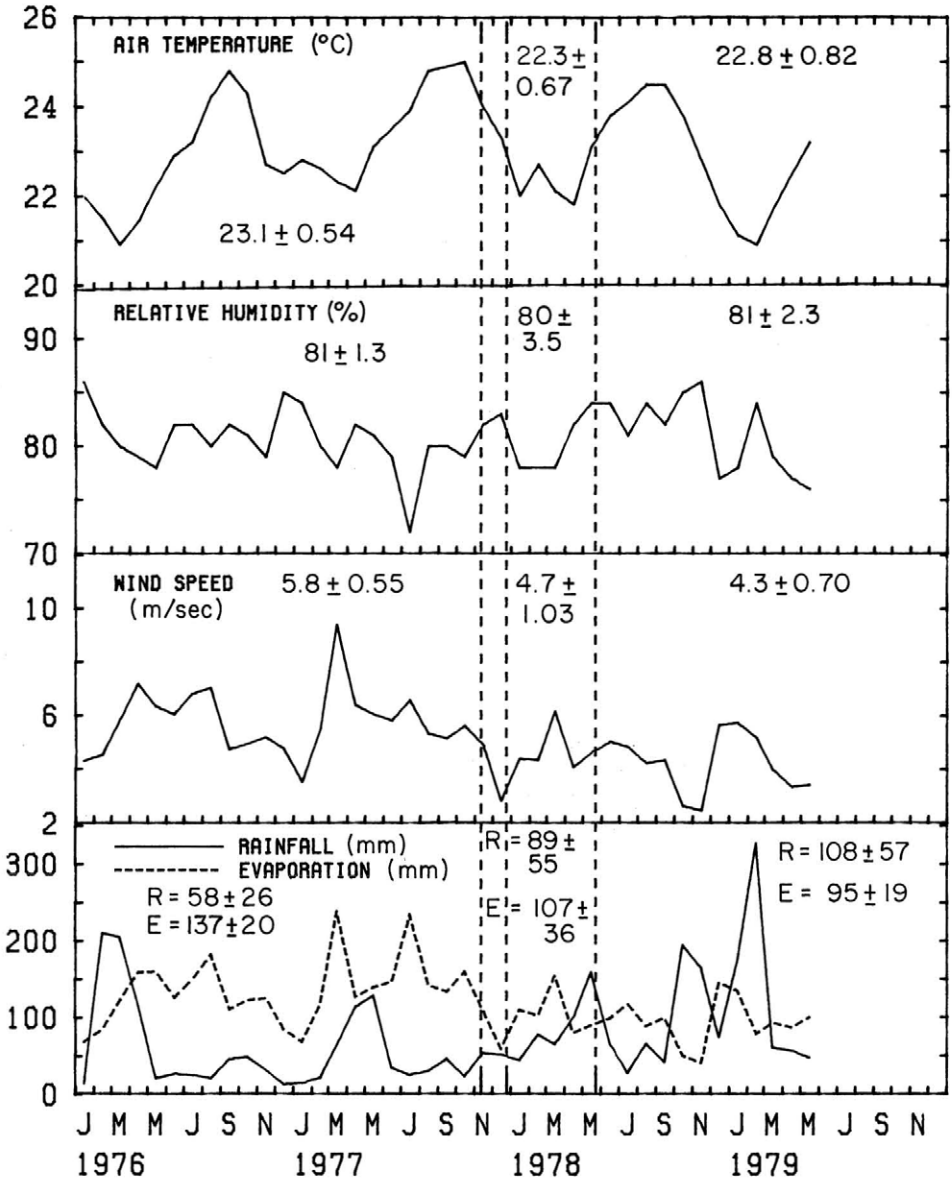


FIGURE 10. Monthly mean ± 95-percent confidence limits of the mean for selected meteorological variables at Coconut Island. In this and subsequent figures, the three vertical dashed lines show the onset of the period during which sewage was shunted between the bay and the ocean, the diversion of the major (Kaneohe) discharge, and the diversion of the Marine Corps discharge.

resent rainfall in the watershed, because those data were highly correlated with gauge data from three other stations in the watershed (Figure 11; Climatological Data, U.S. Department of Commerce). The figure shows a wet season from October to May and a dry season the remainder of the year, although year-to-year differences are large. The prediversion years, 1976 and 1977, were unusually dry, while 1978 and 1979 had

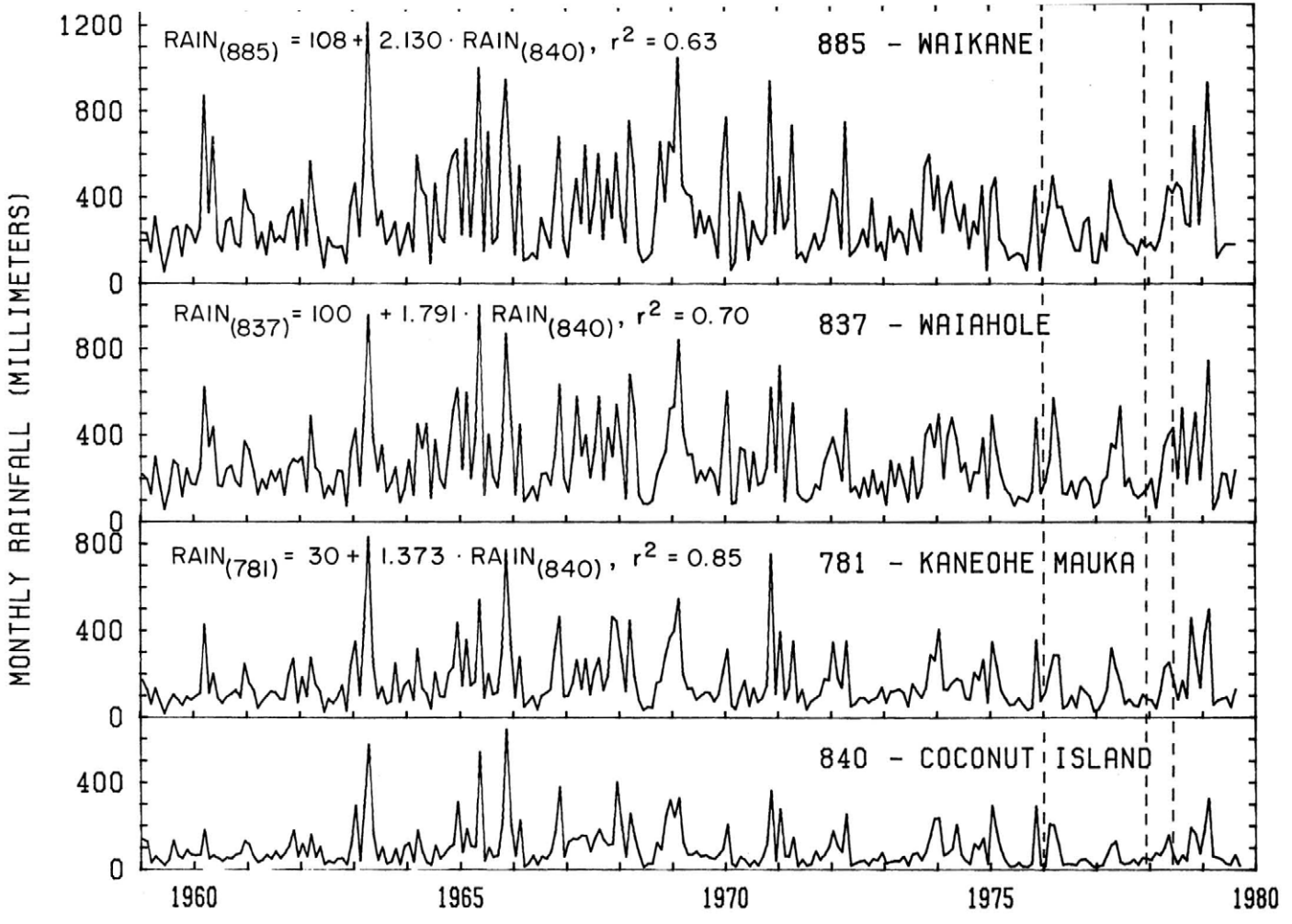


FIGURE 11. Long-term rainfall at selected gauges in the Kaneohe watershed (from U.S. Department of Commerce, Climatological Data, Hawaii and Pacific). The three vertical dashed lines show the beginning of our prediversion period, the diversion of the major (Kaneohe) sewage discharge, and the diversion of the Marine Corps discharge.

TABLE 3

METEOROLOGICALLY-DERIVED LONG-TERM AVERAGE WATER BUDGET FOR INNER KANEOHE BAY

	AREA (km^2)	RAINFALL ($m \cdot yr^{-1}$)	EVAPORATION ($m \cdot yr^{-1}$)	NET WATER ($10^6 m^3 \cdot yr^{-1}$)
Inner bay	31	+ 1.4	− 1.7	− 9
Watershed	97	+ 2.4	− 1.1	+ 126
Entire area	128	+ 2.16	− 1.25	+ 117

normal amounts of rainfall (Figure 10). Evaporation showed the opposite trend, so that there was net evaporation during the prediversion period and slight net rainfall after diversion.

Rainfall sufficient to cause runoff damaging to Kaneohe reefs occurred in May 1965 (Banner 1968, 1974). The months of April 1963, November 1965, and February 1969 received comparable amounts of rain, although no damage to reefs was documented. February 1979 was the wettest month during our study but did not approach the rainfall or runoff extremes experienced in the watershed previously.

Long-term mean rainfall in the watershed is about 2400 $mm \cdot yr^{-1}$, and in the inner bay, 1400. Evapotranspiration averages about 1100 $mm \cdot yr^{-1}$ (Takasaki, Hiroshima, and Lubke 1969), while evaporation in the inner bay is about 1700 $mm \cdot yr^{-1}$. These figures can be combined with watershed and bay areas to calculate that there is an average net input of freshwater to the bay and watershed of $117 \times 10^6 m^3 \cdot yr^{-1}$ (Table 3).

Figure 12 summarizes wind speed and direction at Coconut Island during the study period. Mean speed was about 5 $m \cdot sec^{-1}$, with no strong seasonality. Postdiversion wind speed was generally lower than the speed before sewage diversion. Wind direction also varies, with wind from the northeast blowing approximately half the time. These northeasterly winds are particularly critical to bay circulation and flushing (see Bay Flushing).

Monthly mean incident solar radiation at Coconut Island (Figure 13) shows an annual cycle between about 300 and 500 $ly \cdot day^{-1}$ because of variations in solar elevation and in day length between 11 and 13 hours. Superimposed on that pattern is short-term daily variation due to changes in cloud cover.

Hydrology

The entry of freshwater to Kaneohe Bay plays several major roles in the ecosystem. Freshwater can lower salinity, and if the salinity depression is sufficient, it can be catastrophic to biotic populations in the bay (e.g., Banner 1968, 1974). Moreover, the freshwater sources can carry dissolved and particulate materials that stimulate or intoxicate biota or otherwise directly affect the bay. Particulate load delivery by storm runoff has caused substantial shoaling of the bay (Hollett 1977; Roy 1970). Of more immediate interest to the present investigation, the freshwater sources deliver nutrients to the bay.

Runoff into the bay is directly tied to rainfall. Except for $23 \times 10^6 m^3 \cdot yr^{-1}$ of freshwater diverted out of the watershed (Takasaki, Hiroshima, and Lubke 1969), the net input to the watershed (Table 3) must enter the bay; thus there is a net input of $94 \times 10^6 m^3 \cdot yr^{-1}$.

Rainfall (Figure 11) shows substantial temporal variation. Runoff (Figure 14) follows a similar pattern, with a constant, low flow rate interrupted by storms. Monthly delivery of water can exceed the long-term average at least fivefold, and instantaneous delivery can exceed the long-term average by three orders of magnitude. The effect on salinity of this intense delivery of freshwater can be magnified because the water column becomes strongly stratified. Banner (1968, 1974) documented a dramatic freshwater kill of shallow-water reef organisms by the runoff of May 1965.

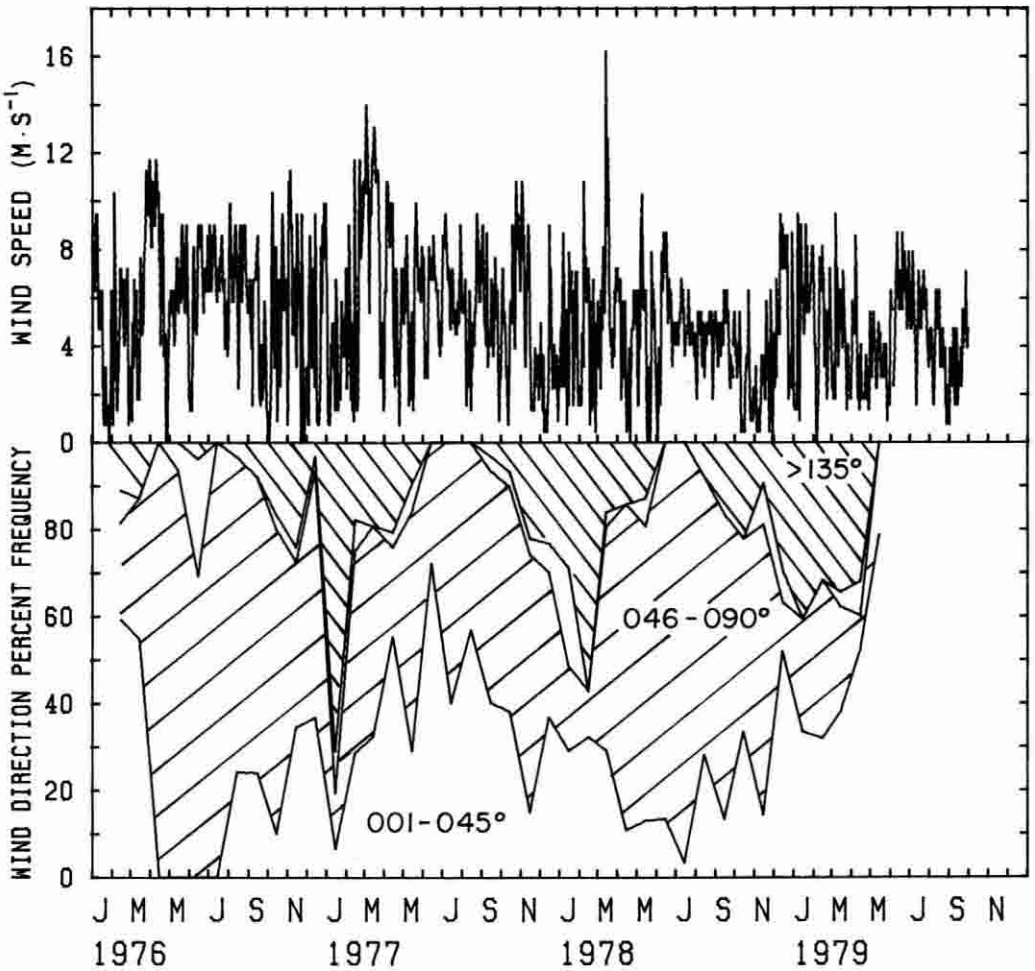


FIGURE 12. Daily mean wind speed and monthly mean wind direction at Coconut Island.

It is useful to examine a water budget for the period of our investigation. The items to be considered in the budgetary analysis are stream flow, groundwater seepage, rainfall and evaporation over the bay itself, and sewage. The budget addressed the four sectors of the bay listed in Table 2. Except for $23 \times 10^6 m^3 \cdot yr^{-1}$ of freshwater diverted from the watershed through tunnels and ditches (Takasaki, Hiroshima, and Lubke 1969), the net rainfall input to the watershed should equal the outflow in streams and groundwater.

Approximately a dozen streams drain from the watershed into Kaneohe Bay. Most of the stream flow enters the NW and OF sectors. Stream flow gauged at three major streams (Figure 9) can be used to estimate total flow to the bay. From Gray and Lau (1973) it can be estimated that the Waikane gauge represents 15 percent of the flow into the NW sector, and the Haiku/Heeia gauge represents 20 percent of the flow into the southern basin, with 80 percent of that flow entering the OF sector. Groundwater seepage, the other major avenue for water entry from the watershed, averages about $22 \times 10^3 m^3 \cdot day^{-1}$ (Sunn et al. 1976).

A simple check on the budget is to compare the long-term average flow calculated

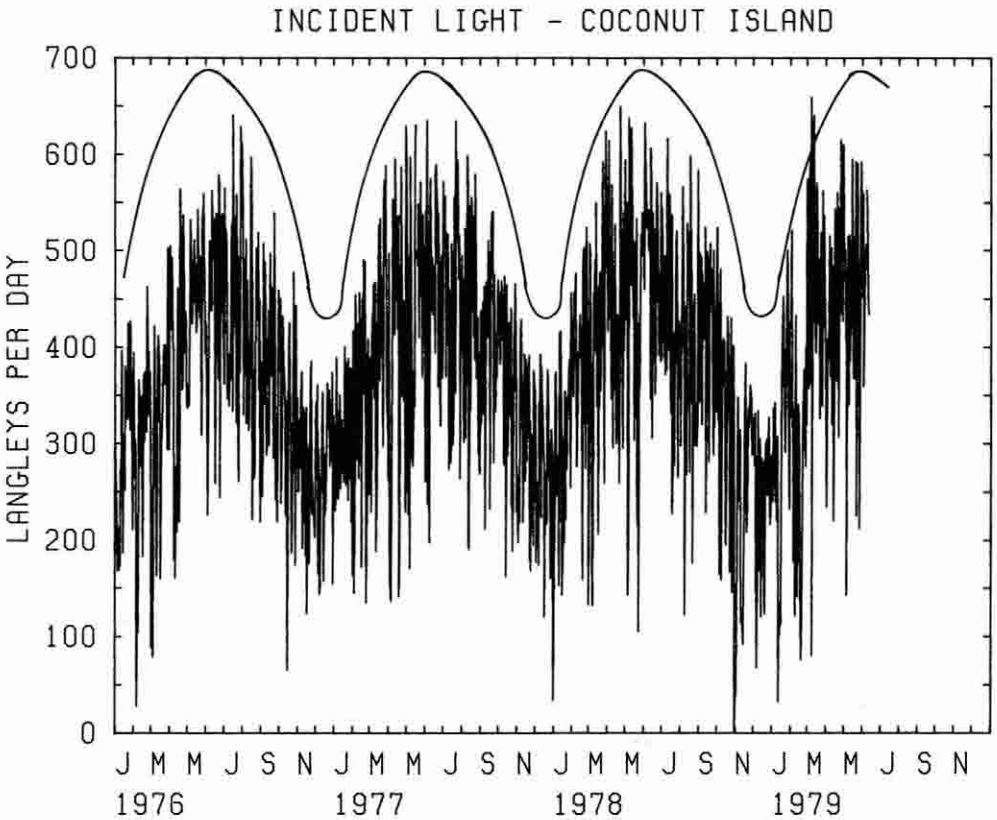


FIGURE 13. Daily solar radiation recorded at Coconut Island during our investigation, with clear-sky radiation (Yoshihara and Ekern 1978) shown for comparison.

by this budget with the meteorologically derived budget. Since Table 4 demonstrates that the long-term water budgets agree within about 7 percent, we can proceed with confidence to shorter-term budgets.

Figure 15 presents the stream flow data, multiplied by the appropriate factors to yield total runoff by sector during our investigation. The prediversion period was abnormally dry, but still retained a vestige of the wet-dry seasonality. By contrast, most of the postdiversion period showed high runoff. Table 5 summarizes the total water budget for the period of our investigation.

That table includes the groundwater flow, assumed (based on the discussion of Takasaki, Hiroshima, and Lubke 1969) to be relatively insensitive to short-term variations in freshwater input to the watershed. Groundwater is assumed to enter the bay sectors in proportion to their shoreline length (Table 2). Rainfall and evaporation over the bay are assumed to be equal to that at Coconut Island (Figure 9) and are prorated according to the areas for each sector given in Table 2. Sewage input of freshwater is taken from Figure 5.

Stream flow dominates the freshwater budget. The average freshwater input increased from 56,000 $m^3 \cdot day^{-1}$ ($20 \times 10^6 m^3 \cdot yr^{-1}$) during the prediversion period to 352,000 $m^3 \cdot day^{-1}$ ($128 \times 10^6 m^3 \cdot yr^{-1}$) during the postdiversion period. By comparison the long-term average freshwater input is 238,000 $m^3 \cdot day^{-1}$ (from Table 5 and inner bay net evaporation).

Most ($\sim$ 60%) of the freshwater runoff enters the NW sector. The OF plus SE

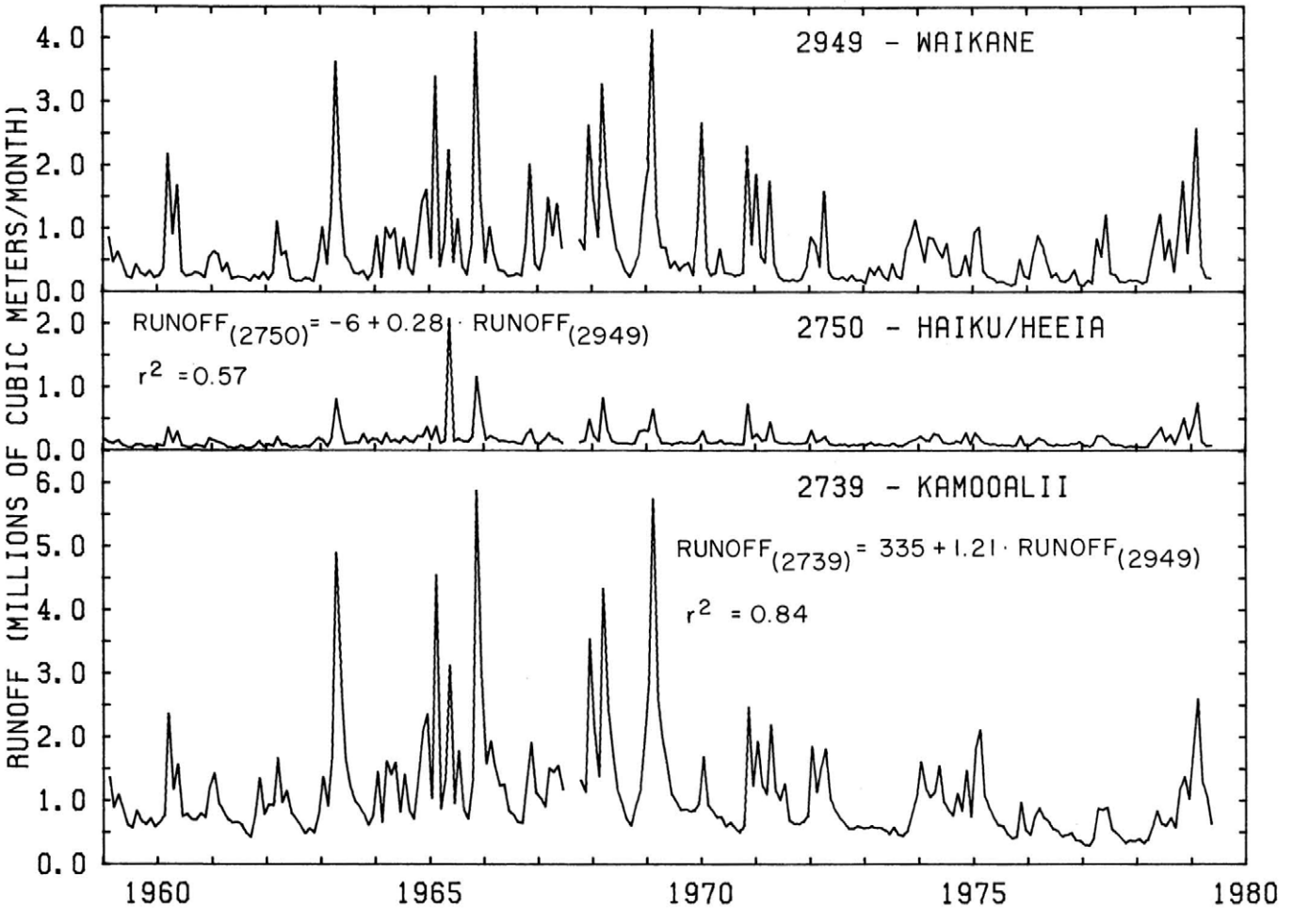


FIGURE 14. Long-term runoff at major streams in Kaneohe watershed. Data from U.S. Geological Survey.

TABLE 4

COMPARISON OF LONG-TERM WATER BUDGETS DERIVED FROM METEOROLOGICAL RECORDS AND STREAM FLOW RECORDS

		NET FLUX ($10^3 m^3 \cdot day^{-1}$)
Meteorological		
Watershed rain minus evaporation (from Meteorology Section)		+ 345
Entry minus exit via tunnels, ditches		− 63
Net		+ 282
Stream Flow		
Waikane ÷ 0.15	(NW)	+ 140
Haiku/Heeia ÷ 0.2	(CE)	+ 28
Kamooalii ÷ 0.5		
·0.2	(SE)	+ 15
·0.8	(OF)	+ 58
Groundwater		+ 22
Net		+ 263

NOTE: See text for explanation of stream flow calculations.

TABLE 5

BUDGET OF FRESHWATER INPUT TO KANEOHE BAY DURING PREDIVERSION AND POSTDIVERSION PERIOD (thousands of $m^3 \cdot day^{-1}$)

	NW	CE	SE	OF	TOTAL
Streams					
pre	82	20	7	30	138
post	197	43	16	59	316
Groundwater	7	7	5	3	22
Rainfall-Evaporation					
pre	−28	−32	−19	−3	−82
post	+5	+5	+3	0	+13
Sewage					
pre	1	0	5	12	18
post	1	0	0	0	1
Total					
pre	62	−5	−2	42	96
post	210	55	24	62	352

sectors (i.e., the southern basin) receive about 25 percent, leaving only 15 percent for the CE sector. At no time during this study did freshwater input approach extremes sufficient to have major impact on the bay. The last time such extremes were realized over large areas of the bay was apparently May 1965 (as documented by Banner 1968, 1974), and the past decade has been markedly drier than the previous decade.

Stream delivery of dissolved nutrients to Kaneohe Bay has been the subject of two recent reports (Lau et al. 1976; Young et al. 1976). We have examined those data for evidence that dissolved nutrient concentrations might depend on flow rate. No such evidence was found, nor did Dugan (1977) find evidence for flow-dependent nutrient concentrations.

Table 6 is our estimate of stream nutrient concentration based on these reports. By contrast with the dissolved-load input, particulate load concentration increases with higher stream flow. Discussion by Bartram (1976) demonstrates that we cannot satisfactorily define suspended-load delivery to the bay as a simple linear function of stream flow. Some undefined power function would be more appropriate. The values in Table 6 were estimated during the prediversion period of our investigation and are assumed to typify the entire period of the investigation. However, it can be demonstrated that they grossly underestimate total particulate organic material delivery by streams as a long-term average.

According to data presented by Lau et al. (1976), particulate organic carbon makes up about 4 percent of the suspended load in the Kaneohe streams. Based on the rate of shoaling of the bay, Hollett (1977) estimated the average long-term delivery of terrigenous sediments to Kaneohe Bay to be about 200 $tons \cdot day^{-1}$. At an average stream flow of 241,000 $m^3 \cdot day^{-1}$ this would yield an average suspended load of 800 $g \cdot m^{-3}$ in stream water. At 4 percent organic carbon, the average particulate carbon content would have to be about 3 $moles \cdot m^{-3}$ for the mean stream flow to provide the observed rate of shoaling. This value is tenfold higher than the observed mean particulate carbon concentration in the streams (Table 6). Clearly the shoaling must result from infrequent storm events, during which large amounts of sediment wash into the bay.

Groundwater composition is assumed to be equivalent to stream composition, except that particulate materials are assumed to be

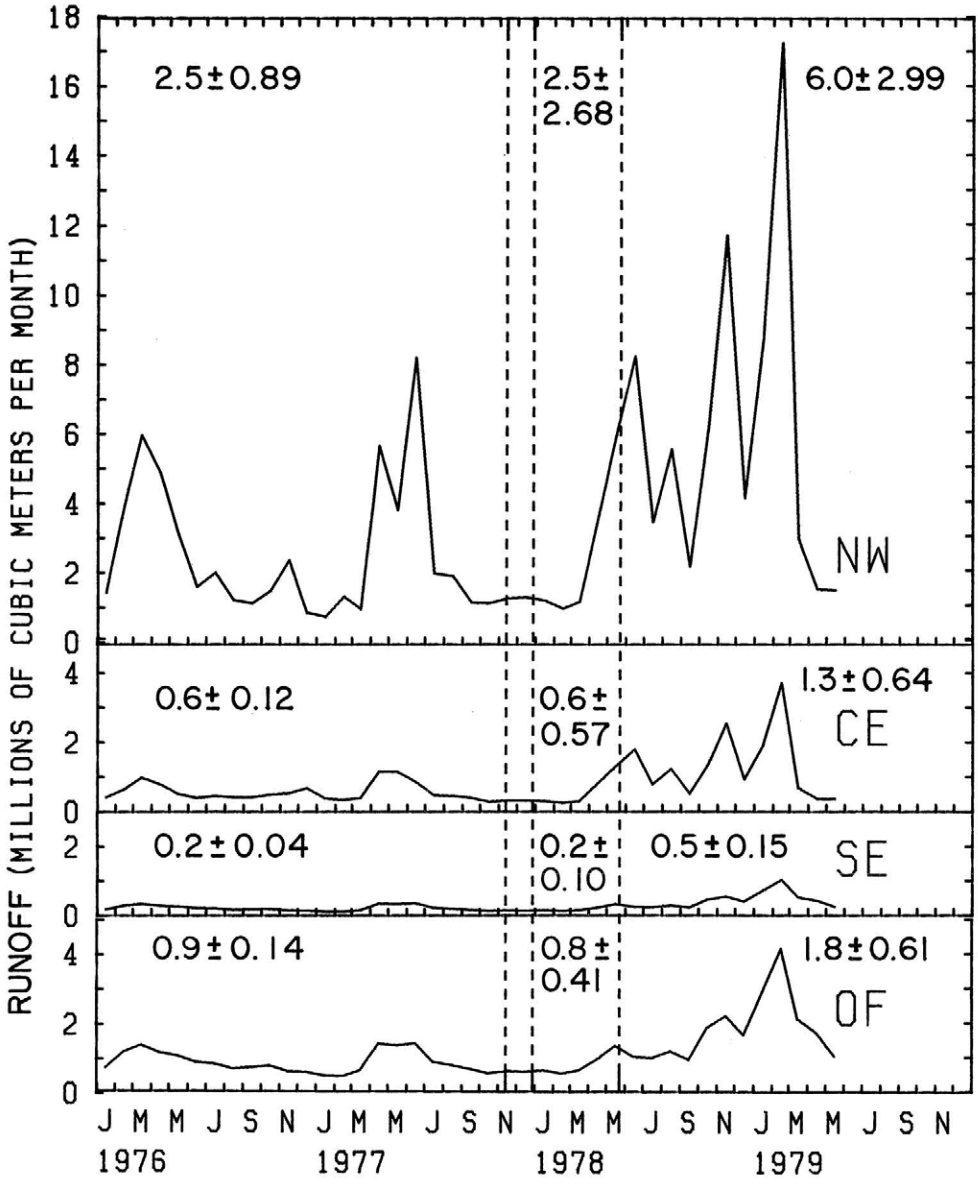


FIGURE 15. Mean runoff for each sector ±95-percent confidence limits of the mean. Vertical dashed lines as in Figure 10.

filtered out of the water. A better assumption (following observations by Johannes 1980, that nitrate in groundwater tends to be elevated) might be that all of the nitrogen becomes oxidized to nitrate. Even with this correction, groundwater apparently makes no more than a small contribution to the bay nutrient budget, especially before sewage diversion.

Direct nutrient input due to rainfall was estimated by measuring dissolved inorganic nitrogen (DIN) concentration in samples of

TABLE 6

APPROXIMATE STREAM DISSOLVED AND PARTICULATE NUTRIENT COMPOSITION
(mmoles·m^{-3})

	NW	CE	SE	OF	FLOW-WEIGHTED AVERAGE
Mean volume flow (10^3m^3·day^{-1})	140	27	14	58	239
Nitrogen					
dissolved inorganic*	10	10	50	50	22
dissolved organic	5	5	25	25	11
particulate	15	25	25	25	19
Total	30	40	100	100	52
Phosphorus					
dissolved inorganic	1.0	0.5	1.5	1.5	1.1
dissolved organic	0.3	0.2	0.5	0.5	0.3
particulate	0.7	0.3	1	1	0.7
Total	2	1	3	3	2.1
Dissolved silicon	500	500	500	500	500
Particulate organic carbon	300	300	300	300	300

NOTE: Estimated from Lau et al. (1976) and Young et al. (1976).
*Stream dissolved inorganic nitrogen is predominantly nitrate.

rainwater. Concentrations had a median of 1.5 mmoles·m^{-3} and a maximum of 18 mmoles·m^{-3}. Although values were highly variable, DIN usually decreased during a heavy rainfall. Since much of the rain input to the bay occurs during storms, the use of the median value is probably conservative. The calculated rate of input based on postdiversion rainfall was 0.16 kmoles·day^{-1}, less than 1 percent of the postdiversion nitrogen input; this source has therefore been ignored in budgetary calculations.

The water budget (Table 5) and the composition of sewage (Table 1) and stream water (Table 6) can be combined to yield estimates of mass loading rates of nutrients and particulate organic materials into Kaneohe Bay under nonstorm conditions. Those results are summarized in Table 7. Note that the nitrogen discharged into the bay decreased by approximately 60 percent in response to sewage diversion and that phosphorus decreased by about 80 percent. The decreases occurred in the OF and SE sectors, with slight increases in the CE and NW sectors from higher postdiversion runoff. Dissolved silicon and particulate organic carbon discharge both increased during the postdiversion period, because these materials are primarily supplied by runoff.

Summary

We have described the physical setting of Kaneohe Bay with the intent of laying a foundation for discussion of our results. Much of the data on the bay can be understood in terms of variation along the two major axes. Along the longitudinal axis we have a general increase in urban influence from north to south, especially in terms of sewage input. We have divided the bay into sectors, primarily on the basis of this gradient. Along the transverse axis we go from a heavy land influence, across coral reefs, and out to the open ocean. We have seen that the delivery of nutrients to the bay via sewage has been superimposed on other sources, notably streams, whose input increased coincidentally with the diversion of sewage. And we have estimated the rates of delivery of nutrients to the various sectors of the bay before and after sewage diversion.

ECOSYSTEM COMPOSITION

Environmental studies are often replete with chemical, biological, and geological composition data, and legislation surrounding environmental impact analysis tends to encourage blind data collection. This section will deal with the composition of Kaneohe Bay, and serves three purposes: First, to provide information that has been used to analyze how this ecosystem works. Second, to give either quantitative or qualitative explanations of the trends seen in the variables examined—whether or not in response to sewage and its diversion. More detailed elaboration and use of the compositional data are presented in the section on Ecosystem Dynamics. Third, to summarize environmental data available for Kaneohe Bay and Oahu that may have potential use beyond the scope of this investigation.

TABLE 7

BUDGET OF DISSOLVED AND PARTICULATE NUTRIENT DELIVERY TO KANEOHE BAY
(kmoles·day^{-1})

	NW	CE	SE	OF	Σ
Prediversion					
Nitrogen					
dissolved inorganic	1.79	0.27	5.10	12.45	19.61
dissolved organic	1.21	0.14	4.10	9.95	15.40
particulate	1.43	0.50	1.18	3.15	6.26
Total	4.43	0.91	10.38	25.55	41.27
Phosphorus					
dissolved inorganic	0.26	0.01	0.87	2.09	3.23
dissolved organic	0.07	0.01	0.21	0.50	0.79
particulate	0.07	0.01	0.06	0.14	0.28
Total	0.40	0.03	1.14	2.73	4.30
Dissolved silicon	45.0	13.5	8.5	22.5	89.5
Particulate organic carbon	25.9	6.0	8.6	24.6	65.1
Postdiversion					
Nitrogen					
dissolved inorganic	2.94	0.50	1.05	3.10	7.59
dissolved organic	1.78	0.25	0.53	1.55	4.11
particulate	3.16	1.08	0.40	1.48	6.12
Total	7.88	1.83	1.98	6.13	17.82
Phosphorus					
dissolved inorganic	0.37	0.03	0.03	0.09	0.52
dissolved organic	0.10	0.01	0.01	0.03	0.15
particulate	0.15	0.01	0.02	0.06	0.24
Total	0.62	0.05	0.06	0.18	0.91
Dissolved silicon	102.5	25.0	10.5	31.0	169.0
Particulate organic carbon	60.4	12.9	4.8	17.7	95.8

The data base presented here includes our own field sampling and laboratory analysis from February 1976 through August 1979; our sampling and analytical methods are presented in the Appendix. We have also drawn heavily from published papers, theses and other unpublished internal reports, published data summaries released by government agencies, and unpublished data to which we had access.

Water Composition

We consider water composition from three vantages: First, we compare composition among our various sampling sites (the OF, SE, CE, and NW stations; Figure 16) within the bay, and to the extent data are available, we compare bay composition with that of the adjacent ocean. Except for a few unavoidable data gaps during our 1976–1979 study, the time-trend data arrays for Kaneohe Bay presented in this section represent samples gathered at least twice monthly, and sometimes as frequently as every day. Unless specified to the contrary, means of the 1-m and 8-m data are used in the analyses.

Second, we compare the bay composition during the prediversion period of our study with the postdiversion composition. Composition during the interim period, when one of the two major sewage discharges had been diverted (January–June 1978) is presented but not discussed, and composition during the November–December 1977 period of alternating discharge and diversion is shown on the graphs but not analyzed.

Third, for selected variables, we discuss the limited arrays of historical data for water composition that could be located to cover approximately the last twenty years. Such

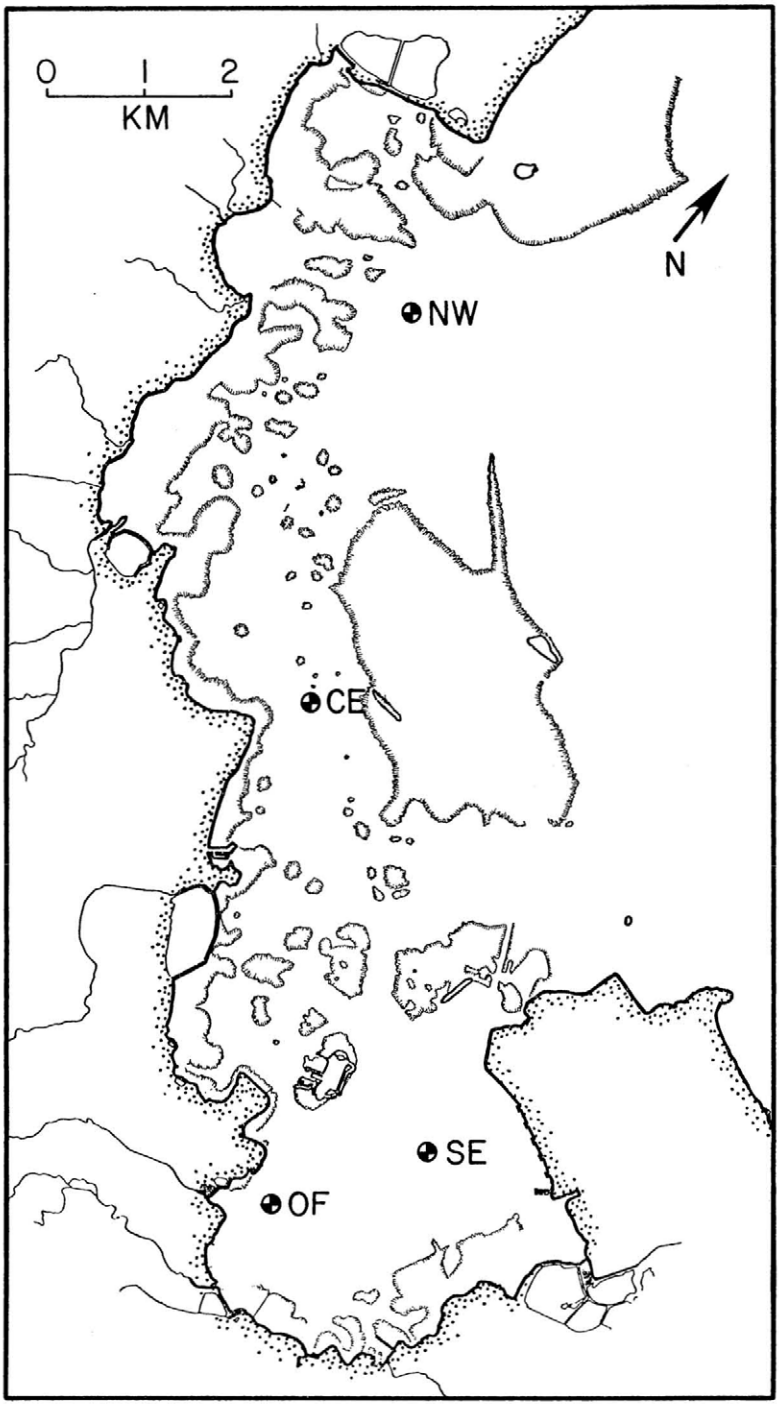


FIGURE 16. Sites of water composition sampling, phytoplankton sampling, and zooplankton sampling, 1976–1979.

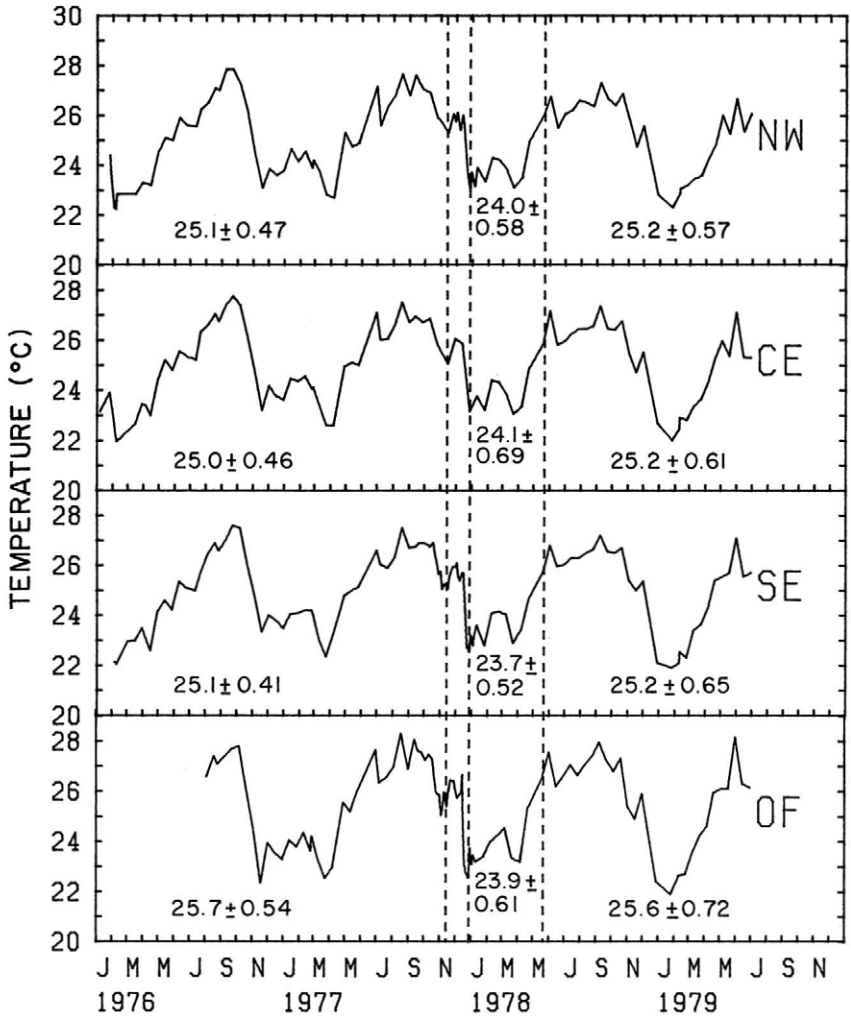


FIGURE 17. Depth-averaged water temperature in Kaneohe Bay. Mean ±95-percent confidence limits of the mean. Vertical dashed lines as in Figure 10.

data arrays might serve to illustrate long-term shifts that have occurred in water composition. Perhaps as important, the arrays presented here illustrate the inadequacy of our knowledge about the compositional variability of this ecosystem (and many others) through time.

TEMPERATURE: Water temperature is likely to play a significant role in any ecosystem by affecting biochemical rates within the system. It can also be useful as a tracer of physical processes.

In Kaneohe Bay, temperature oscillates seasonally about a mean of 25.1° C with an annual range of 3.8° C (Figure 17). The seasonal pattern consists of a gradual warming from March, the coldest month, to September, the warmest, followed by rapid cooling to a relatively stable winter temperature.

Comparison of our Kaneohe Bay temperature data with data from an oceanic recording station (Seckel and Yong 1977) yields the following relationship:

$$T_{\text{Bay}} = -11.85 + 1.50 \cdot T_{\text{Ocean}},\ r^2 = 0.71$$

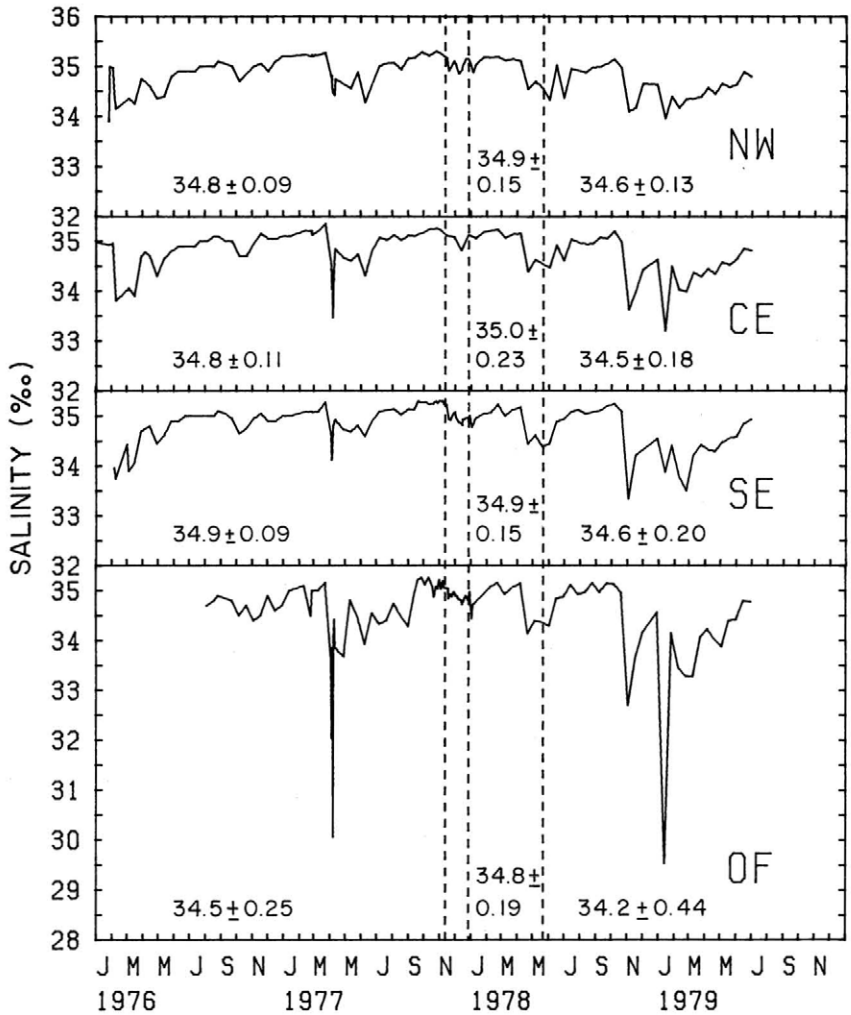


FIGURE 18. Depth-averaged salinity in Kaneohe Bay. Mean ±95-percent confidence limits of the mean. Vertical dashed lines as in Figure 10.

The mean temperature in the bay is about 0.7° C higher than that in the ocean. The bay cools below ocean temperatures in the winter, and warms above ocean temperatures in the summer, reflecting the response of a partly enclosed water mass to changing heat flux. The bay exports heat to the ocean in spring and summer, imports heat in the fall, and is in balance in the winter (see also Bathen 1968).

SALINITY: Salinity variations in an estuarine system are the primary proximate cause of variable water density, which in turn plays a role in water stratification and circulation (see Bay Flushing). Lowered salinity can depress the metabolic rates or reduce the survival of marine organisms. Finally, salinity variations can be used as indicators of variable freshwater inputs and as water-mass tracers.

Depth-averaged bay salinity (Figure 18) remained near the oceanic average of 35‰ most of the time, with frequent slight depres-

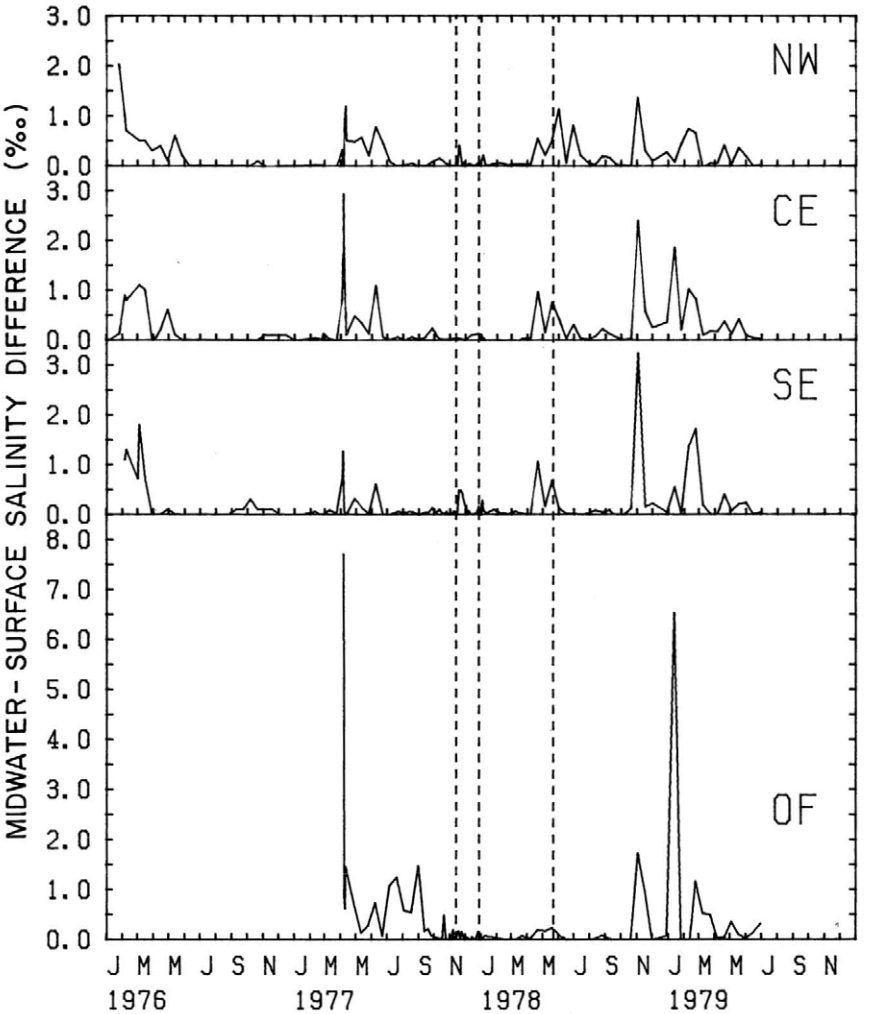


FIGURE 19. Differences between surface and midwater salinity due to runoff and stratification. Vertical dashed lines as in Figure 10.

sions related to increased runoff. These depressions never went below 33‰ except twice at the OF station. Surface salinity, of course, showed much larger excursions. Figure 19 illustrates the frequency of stratification induced by rainfall and runoff.

In principle it should be possible to use the bay and ocean data and the water budget of the bay and its watershed to calculate a salt budget for the bay. Two practicalities preclude this. During our study the average salinity differences among our four stations and between the bay and the ocean were 0.4‰ or less—too small a differential to be reliably quantified from only four stations. Secondly, salinity (and density) stratification (Figure 19) can result in a low-salinity surface layer that escapes the bay more rapidly than the average bay-ocean exchange.

The failure of the surface layer to mix vertically can have profound and disastrous results in terms of reef-flat "kills" of reef organisms (Banner 1968, 1974), but the maximum salinity excursions encountered during

this investigation (to 29‰) are well within the range tolerated by reef organisms (e.g., Smith et al. 1979).

OXYGEN AND CARBON DIOXIDE: Oxygen content of bay water is of interest because it can be used as a tracer of biochemical processes and because low oxygen levels can impose stress on the biota. Oxygen concentrations were compared with saturated values calculated from the temperature and salinity data (Weiss 1970). The sector-weighted mean saturation for January 1976 to June 1977 was 98 percent, with the lowest mean value of 94 percent at station OF. There was little variation among sectors, and these levels do not impose a metabolic stress. We therefore discontinued routine oxygen analyses of the water column.

The carbon dioxide content of seawater includes dissolved free CO_2 and dissolved ionic species (HCO_3^- and $CO_3^=$). The value of each component of the CO_2 system is calculable from pH, alkalinity, salinity, and temperature (Skirrow 1975). pH and specific alkalinity in 1976–1977 varied little from the bay-wide means of 8.31 and 0.116, respectively. Therefore the only further use of CO_2 was as a tracer of metabolic processes on reef flats (see Metabolism).

NITROGEN: Nitrogen is a major nutrient utilized in metabolic processes and biochemical reactions. Its abundance in surface seawater is ordinarily low, so the levels of availability are of specific importance to biological activity (Redfield, Ketchum, and Richards 1963; Spencer 1975). It is of further interest to this study, because the supply of nitrogen to the bay was a significant function of sewage discharge and was substantially altered by the diversion of sewage (Table 7).

We routinely measured four categories of nitrogen: nitrate (actually $NO_3^- + NO_2^-$; NO_2^- is ordinarily minor), ammonium, dissolved organic nitrogen, and particulate nitrogen. The sum of these categories is called total nitrogen; it is actually total fixed nitrogen and excludes the large pool of gaseous N_2 dissolved in seawater (≈ 0.8 mole$\cdot$m^{-3}; Weiss 1970). We will also refer to dissolved inorganic nitrogen (nitrate + ammonium), which is considered to be the pool of nitrogen most readily available for plant uptake. Nitrate is derived mainly from stream runoff (Table 6), while ammonium is both the principal form of nitrogen in sewage (Table 1) and the principal form of internally recycled nitrogen. Dissolved organic nitrogen includes several compounds, of which only urea and free amino acids are readily available for plant uptake (see, e.g., McCarthy 1972), although other forms may be available to bacteria. Particulate nitrogen is the nitrogen fraction of the particulate organic materials in the water and includes land-derived detritus, detritus produced by the metabolism and death of organisms within the water, and the organisms themselves.

Figure 20 and Table 8 summarize the fixed nitrogen data gathered during our investigation. Prediversion nitrate and ammonium were higher at the OF station than elsewhere, whereas postdiversion dissolved inorganic nitrogen showed less variation among sectors. We tested for shifts in ammonium, nitrate, dissolved organic nitrogen, and particulate nitrogen using an analysis of covariance for the data from each station. The covariate used was a cosine plus sine term with an annual period for the first three variables, and the short-term wind factor (see Appendix: Environmental Variability) for particulate nitrogen; these were the only significant covariates. The results (Table 8) show significant decreases in nitrate, ammonium, and particulate nitrogen, and increases in dissolved organic nitrogen, at all stations except NW.

Available historical data on inorganic nitrogen concentrations are scanty and show no trends. Krasnick (1973) suggested that the bay might show elevated nitrate levels from wet-season runoff, but the historical data are insufficient to show this effect. Historical phosphate data (below) are more complete and better suited to determine long-term trends in nutrient concentration changes within the bay.

Oceanic values for nitrate and ammonium (Table 8) are available from Laws (1980). The data suggest that nitrate is lower off-

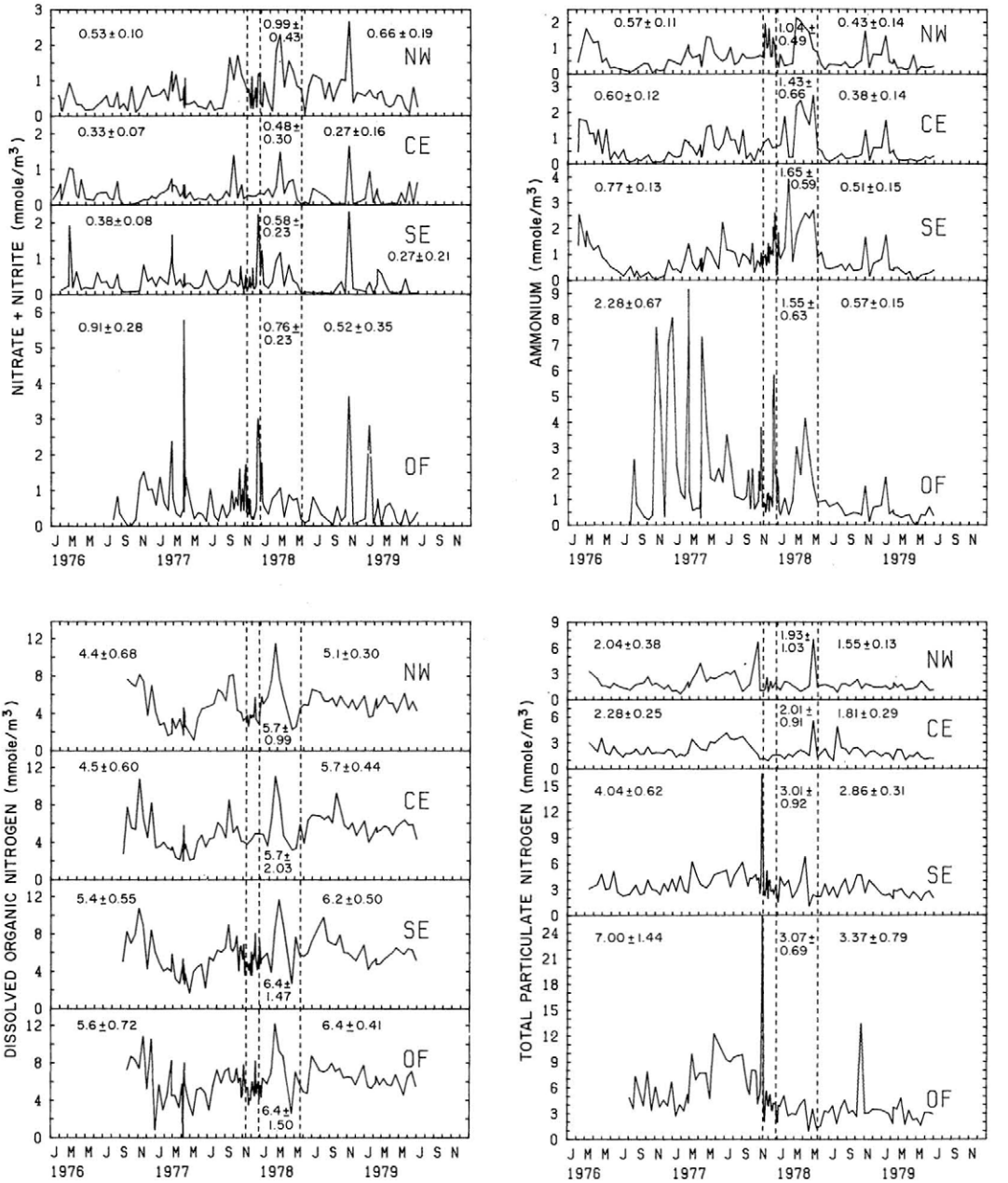


FIGURE 20. Nitrogen concentrations in the four sectors, mean ±95-percent confidence limits of the mean. Vertical dashed lines as in Figure 10.

TABLE 8

TOTAL FIXED NITROGEN INVENTORY IN KANEOHE BAY
(mmoles · m^{-3})

SECTOR VOLUME ($10^6 m^3$)	NW 66.41	CE 119.68	SE 74.24	OF 5.35	BAY MEAN* 265.68	OCEAN†
Dissolved inorganic nitrogen						
Nitrate + nitrite						
pre	0.53	0.33‡	0.38§	0.91§	0.41	0.14
post	0.66	0.27	0.27	0.52	0.37	
percent change	25	− 18	− 29	− 43	− 10	
Ammonium						
pre	0.57	0.60‡	0.77‡	2.28§	0.67	0.47
post	0.43	0.38	0.51	0.57	0.43	
percent change	− 25	− 37	− 34	75	− 36	
Subtotal						
pre	1.10	0.93	1.15	3.19	1.08	0.61
post	1.09	0.65	0.78	1.09	0.80	
percent change	− 1	− 30	− 32	− 66	− 26	
Dissolved organic nitrogen						
pre	4.4	4.5§	5.4§	5.6‡	4.7	4.5
post	5.1	5.7	6.2	6.4	5.7	
percent change	16	27	15	14	21	
Particulate nitrogen						
pre	2.04	2.28‡	4.04§	7.00§	2.80	0.44
post	1.55	1.81	2.86	3.37	2.07	
percent change	− 24	− 21	− 29	− 52	− 26	
Total Nitrogen						
pre	7.5	7.7	10.6	15.8	8.6	5.6
post	7.7	8.2	9.8	10.9	8.6	
percent change	3	6	− 8	− 31	0	

*Weighted by sector volume.
†From Laws (1980), except dissolved organic nitrogen (unpublished data from J. Szyper).
‡Results of tests of significance of decrease with diversion (analysis of covariance; see text), $p < 0.05$.
§Results of tests of significance of decrease with diversion, $p < 0.01$.

shore than in the bay; ammonium shows little difference between offshore and the bay. Mean total inorganic nitrogen percentage decreases for the stations are given in Table 8.

Dissolved organic nitrogen values (Figure 13, Table 8) are much higher than inorganic nitrogen. There is little spatial trend within the bay; increases with sewage diversion are superimposed on a small but significant seasonal cycle. Dissolved organic nitrogen in the bay is apparently elevated slightly above that in the ocean, although the information for comparison is very scanty.

Particulate nitrogen shows a gradient from OF to SE to the CE and NW stations (Figure 13, Table 8). The gradient decreased, but did not disappear, after sewage diversion. Mean particulate nitrogen values decreased at all stations. A very slight but significant seasonal trend was present. The average bay particulate nitrogen level is 5 to 6 times greater than the coastal oceanic level. Particulate nitrogen showed the largest gradient within the bay and between the bay and the ocean. The proportional decreases of particulate and dissolved nitrogen were about equal at each station except NW. The only significant historical data base is for nitrate, which is not a particularly sensitive indicator of nitrogen loading. Dissolved organic nitrogen, the single most abundant form of nitrogen, is also the most poorly

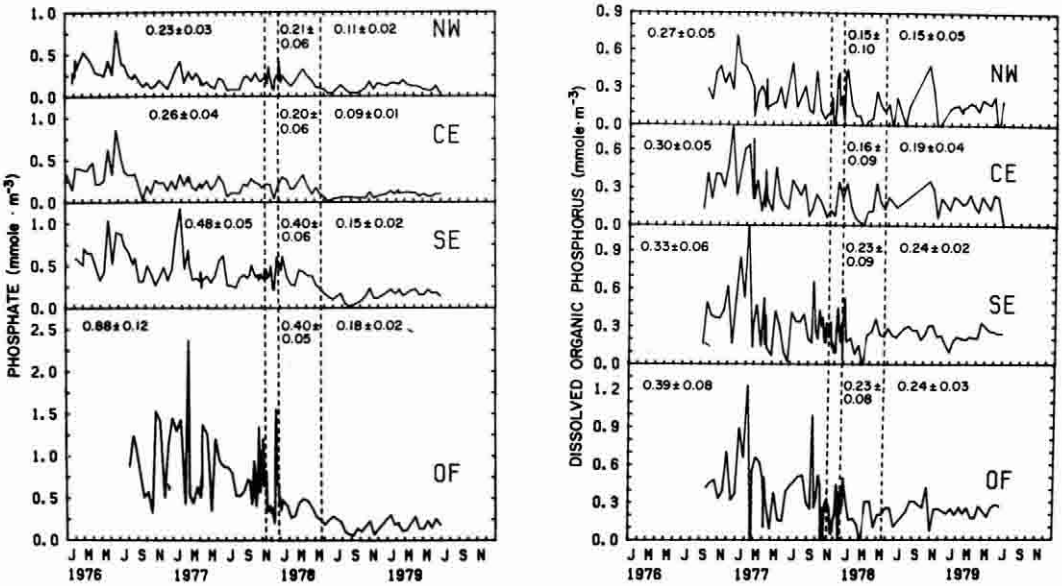


FIGURE 21. Phosphorus concentrations in the four sectors, mean ±95-percent confidence limits of the mean. Vertical dashed lines as in Figure 10.

TABLE 9

TOTAL PHOSPHORUS INVENTORY IN KANEOHE BAY
(mmoles · m^{-3})

SECTOR VOLUME ($10^6 m^3$)	NW 66.41	CE 119.68	SE 74.24	OF 5.35	BAY MEAN* 265.68	OCEAN†
Dissolved inorganic						
pre	0.23	0.26	0.48	0.88	0.33	0.13
post	0.11	0.09	0.15	0.18	0.11	
Dissolved organic						
pre	0.27	0.30	0.33	0.39	0.30	0.30
post	0.15	0.19	0.24	0.24	0.20	
Particulate						
pre	0.08	0.09	0.20	0.38	0.12	0.01
post	0.05	0.06	0.13	0.16	0.08	
Total						
pre	0.58	0.65	1.01	1.65	0.75	0.44
post	0.31	0.34	0.52	0.58	0.39	

*Weighted by sector volume.
†From Laws (1980), except dissolved organic phosphorus (assembled from various sources).

known. Mainly because of this large and poorly defined component, the bay-wide total nitrogen inventory did not change demonstrably in response to sewage diversion.

PHOSPHORUS: Phosphorus is another nutrient used in metabolic processes and provided in quantity by sewage discharge. Like nitrogen, phosphorus tends to be present in low concentrations in surface seawater (Spencer 1975).

Two categories of phosphorus were routinely measured during this study: dissolved inorganic phosphorus (phosphate)

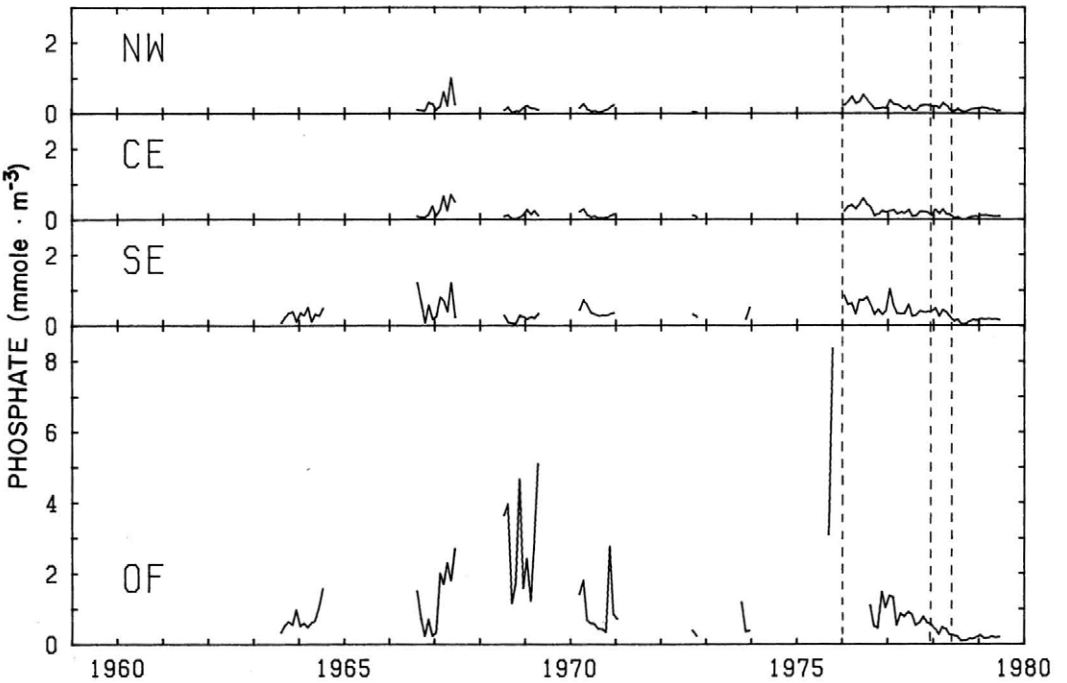


FIGURE 22. Long-term phosphate data for Kaneohe Bay. Compiled from Bathen (1968), Krasnick (1973), Piyakarnchana (1965), Schell (unpublished), Szyper (unpublished), Young et al. (1973), and our own data. Vertical dashed lines as in Figure 11.

and dissolved organic phosphorus. A third category, particulate phosphorus, is inferred from a more limited data set by regression against the particulate nitrogen data. The sum of these is total phosphorus.

Figure 21 and Table 9 summarize the data for dissolved and particulate phosphorus. Inorganic phosphorus showed a gradient from the OF station to the NW sector before sewage diversion; that gradient almost vanished after diversion. The data do not suggest any pattern of seasonality. Figure 22 summarizes the limited historical data for inorganic phosphorus. There is a hint at the OF station of an increase in inorganic phosphorus after the addition of sewage; the earliest data presented from that sector (from Piyakarnchana 1965) were collected during the first year of operation of the Kaneohe sewage treatment plant (see Population Growth and Sewage Discharge). As with nitrate, the long-term data base for inorganic phosphorus is too fragmented to ascertain whether the sporadic high values represent faulty data or real variability. Based on the postdiversion concentration of inorganic phosphorus and subsequent work by Atkinson (1981), we believe that presewage inorganic phosphorus levels were probably near or slightly below oceanic levels.

Dissolved organic phosphorus levels before sewage diversion were apparently near oceanic levels, dropping below them after diversion. As with dissolved organic nitrogen, dissolved organic phosphorus is not well defined. However, dissolved organic phosphorus does not quantitatively dominate the phosphorus pool in the same manner that dissolved organic nitrogen dominates the nitrogen pool.

Particulate phosphorus data were not gathered routinely because of difficulties in developing and testing a satisfactory analytical technique. Those difficulties have been largely overcome, and both pre- and postdiver-

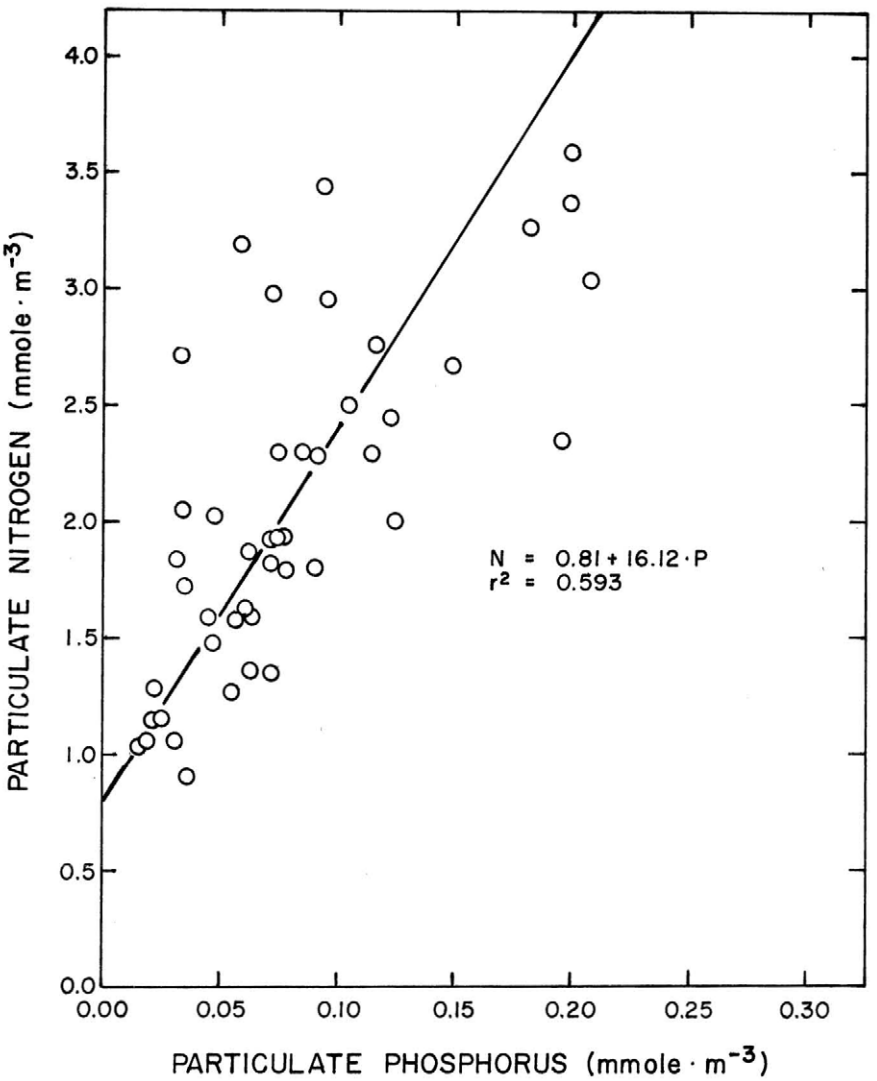


FIGURE 23. Particulate organic phosphorus versus nitrogen in Kaneohe Bay suspended load.

sion particulate phosphorus levels can be inferred from the regression relationship between particulate phosphorus and nitrogen (Figure 23). In general, the particulate phosphorus values inferred from particulate nitrogen were relatively low, usually constituting less than 20 percent of the total phosphorus. There was a large proportional difference between oceanic and bay particulate phosphorus levels, but the bay-to-ocean difference in total phosphorus was dominated by the dissolved inorganic and organic phosphorus differences. The bay-wide inventory of phosphorus dropped by about a factor of two after sewage diversion. Despite the limitations imposed by the historical data (Figure 22), it seems safe to conclude that total phosphorus levels before significant sewage loading into the bay were probably rather close to or even below oceanic levels. Particulate phosphorus is the most likely exception to this generality.

TABLE 10

DISSOLVED SILICON INVENTORY IN KANEOHE BAY
(mmoles · m^{-3})

SECTOR	NW	CE	SE	OF	BAY MEAN*	OCEAN†
VOLUME ($10^6 m^3$)	66.41	119.68	74.24	5.35	265.68	
Dissolved silicon						
pre	7.2	6.6	8.6	11.5	7.4	7.0
post	8.1	9.1	11.9	15.5	9.8	

*Weighted by sector volume.
†From Laws (1980).

TABLE 11

INVENTORY OF PARTICULATE ORGANIC CARBON AND CHLOROPHYLL IN KANEOHE BAY

SECTOR	NW	CE	SE	OF	BAY MEAN*	OCEAN†
VOLUME ($10^6 m^3$)	66.41	119.68	74.24	5.35	265.68	
Carbon (mmoles · m^{-3})						
pre	22.4	20.2	26.4	38.2	22.8	3.58
post	14.2	12.7	17.5	17.3	14.5	
Chlorophyll (mg · m^{-3})						
pre	0.68	0.81	1.78	4.67	1.13	0.20
post	0.55	0.60	1.23	1.33	0.78	

*Weighted by sector volume.
†From Laws (1980).

SILICON: The remaining nutrient for which we have some data, silicon (or dissolved silicate), is of interest specifically because it was not supplied in significant quantity by sewage. Silicon concentrations were highest at the OF station (Table 10). The low-runoff prediversion period had dissolved silicon levels near oceanic levels, whereas the values were above oceanic levels during the post-diversion period.

PARTICULATE ORGANIC MATERIALS: Particulate materials in bay water include land-derived sediments, particulate $CaCO_3$ which is of marine origin, organic detritus, and plankton. In this section we consider various aspects of particulate organic material, which includes both detrital material and plankton, but (as the section on Biotic Composition demonstrates) detritus for the most part dominates.

The data for particulate nitrogen and phosphorus have been presented already in Tables 8 and 9. Particulate carbon is shown in Figure 24 and chlorophyll in Figure 25, while means for both appear in Table 11.

For each of the materials, there was a substantial (> 50%) drop in concentration at the OF station after sewage diversion. Each showed a strong gradient of decreasing concentration away from OF before sewage diversion and a lesser gradient after diversion; and each was higher in the bay, both before and after diversion, than in the adjacent oceanic waters.

Some historical data are available for chlorophyll (Figure 26). The data suggest that the chlorophyll levels were lower than any prediversion values before sewages discharge began in 1963 but that shortly after inception of sewage discharge, the values climbed (data from Piyakarnchana 1965). This pattern can be observed with some confidence only at the OF station. As with other variables, historical data are insufficient for us to draw long-term conclu-

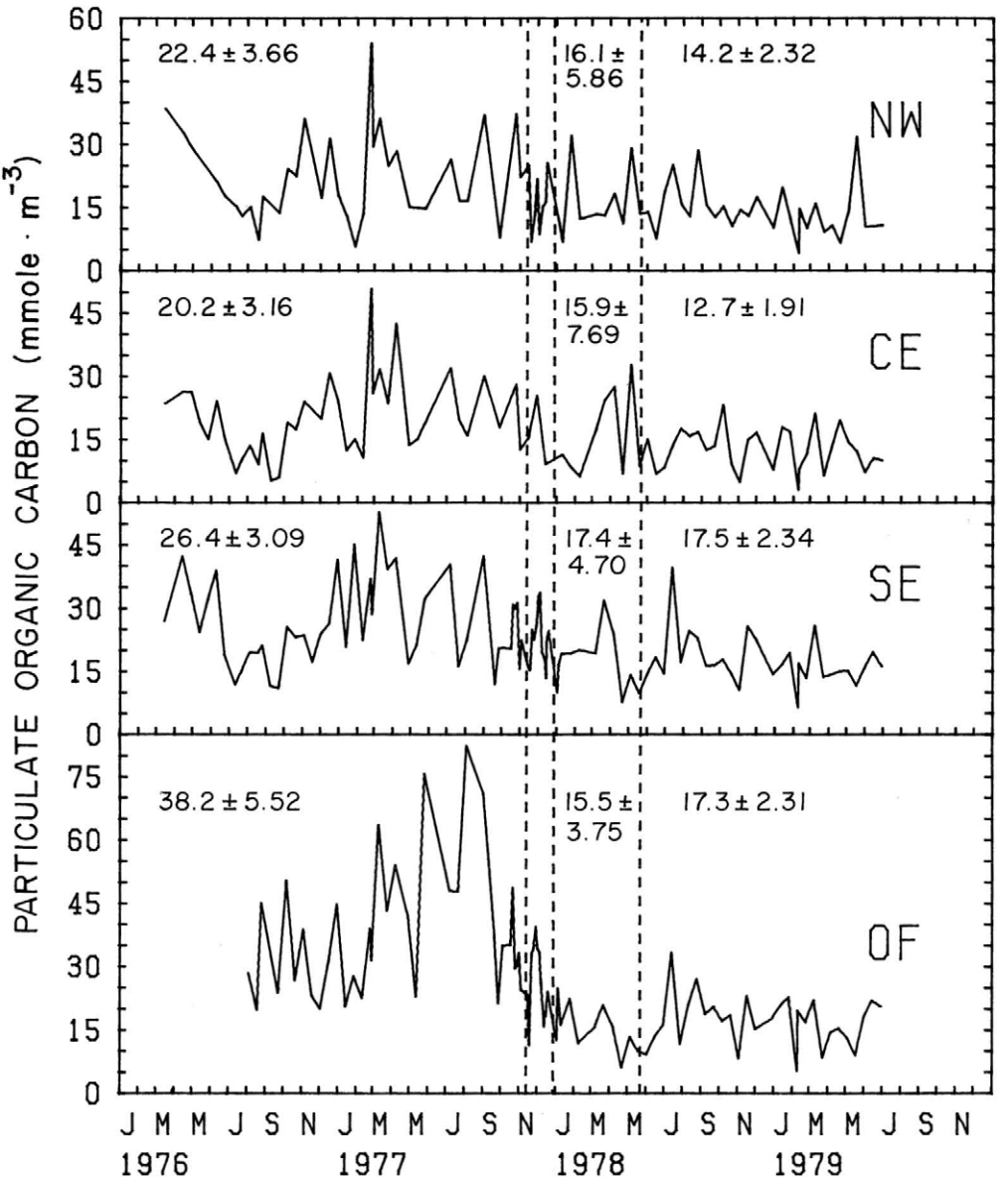


FIGURE 24. Particulate organic carbon in the four sectors, mean ±95-percent confidence limits of the mean. Vertical dashed lines as in Figure 10.

sions for the other stations. We infer from the postdiversion decrease of chlorophyll throughout the bay (Figure 25) that the entire bay showed some response to inception of sewage discharge. It seems evident, however, and can be inferred from a statement by Tester (1951), that the waters of Kaneohe Bay have historically maintained some elevation of particulate materials above the levels encountered along the open coast. At present, particulate organic materials in the bay are elevated four or more

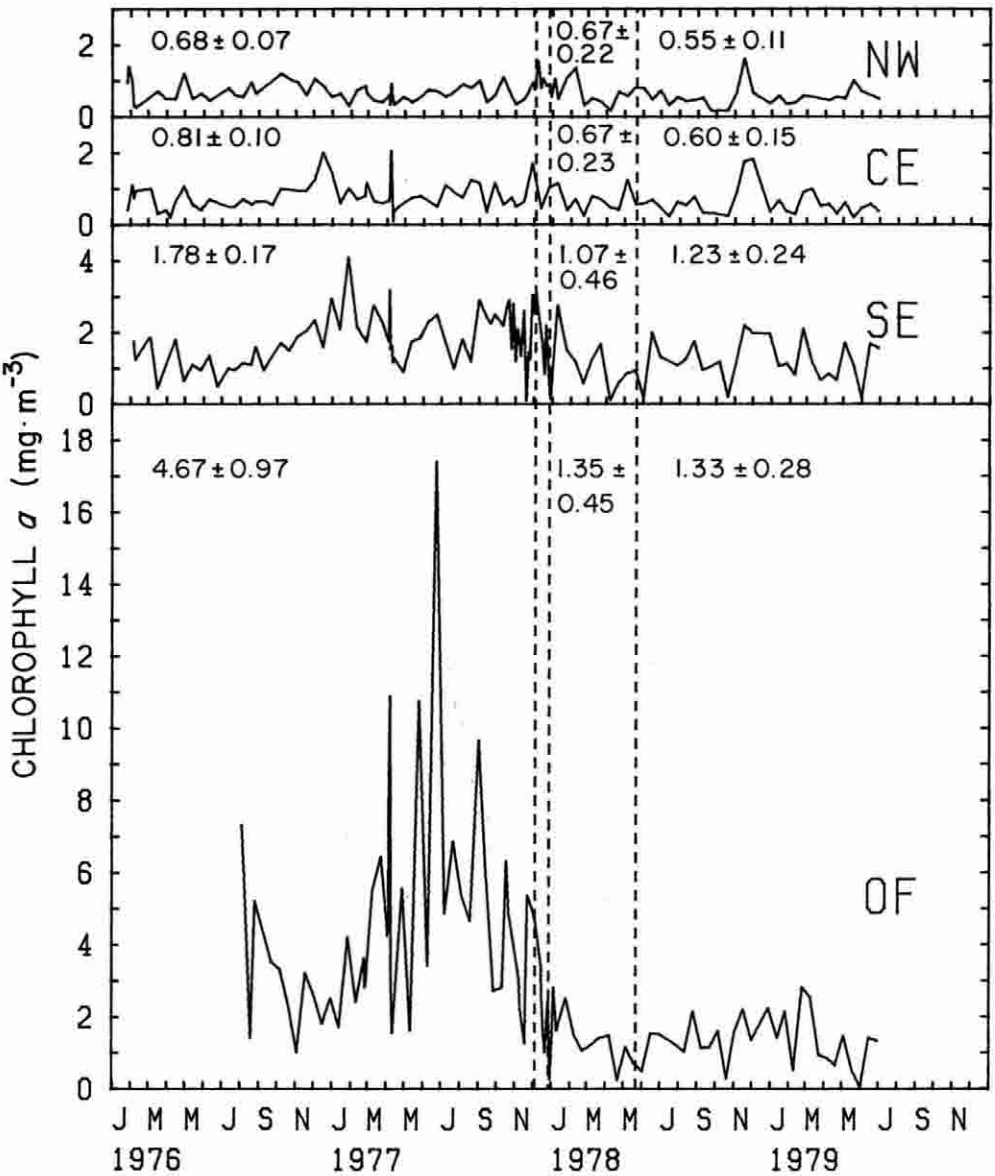


FIGURE 25. Chlorophyll-*a* in the four sectors, mean ±95-percent confidence limits of the mean. Vertical dashed lines as in Figure 10.

times above oceanic levels. These conditions probably closely approximate presewage conditions.

WATER CLARITY: Two different measures of water clarity were made routinely during this investigation: Secchi depth readings and depth-averaged light transmissometer measurements. The Secchi depths (D, meters) were converted to extinction coefficients (k, m^{-1}) by the empirical relationship:

$$k = 1.7/D \quad (1)$$

This old (Poole and Atkins 1929) relation-

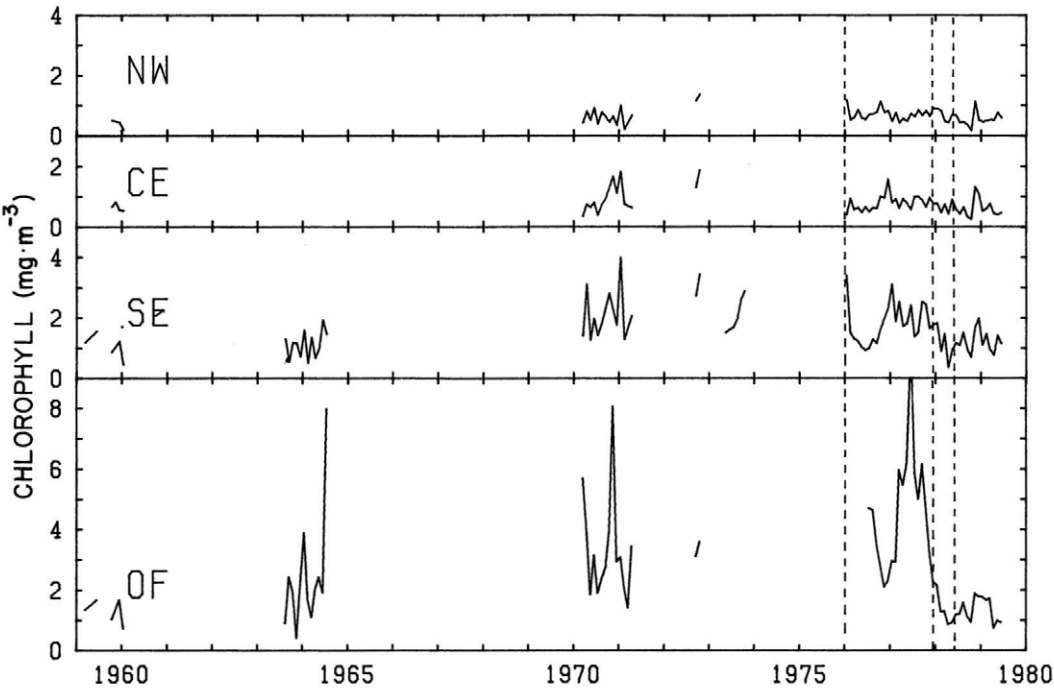


FIGURE 26. Long-term chlorophyll data from Kaneohe Bay. Data from Doty and Capurro (1961), Krasnick (1973), Lamberson (1974), Piyakarnchana (1965), Szyper (unpublished), and our own data set. Vertical dashed lines as in Figure 11.

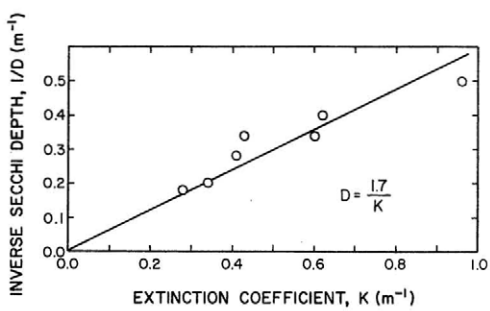


FIGURE 27. Extinction coefficient versus inverse Secchi depth.

TABLE 12

MEAN VALUES ± 95-PERCENT CONFIDENCE LIMITS OF EXTINCTION FROM ALL SOURCES AT EACH STATION, PRE- AND POSTDIVERSION, WITH PERCENT DECREASE WITH SEWAGE DIVERSION

STATION	PREDIVERSION	POSTDIVERSION	% DECREASE
NW	0.29 ± 0.02	0.25 ± 0.02	14
CE	0.28 ± 0.02	0.23 ± 0.02	18
SE	0.37 ± 0.02	0.29 ± 0.02	22
OF	0.59 ± 0.04	0.41 ± 0.04	31

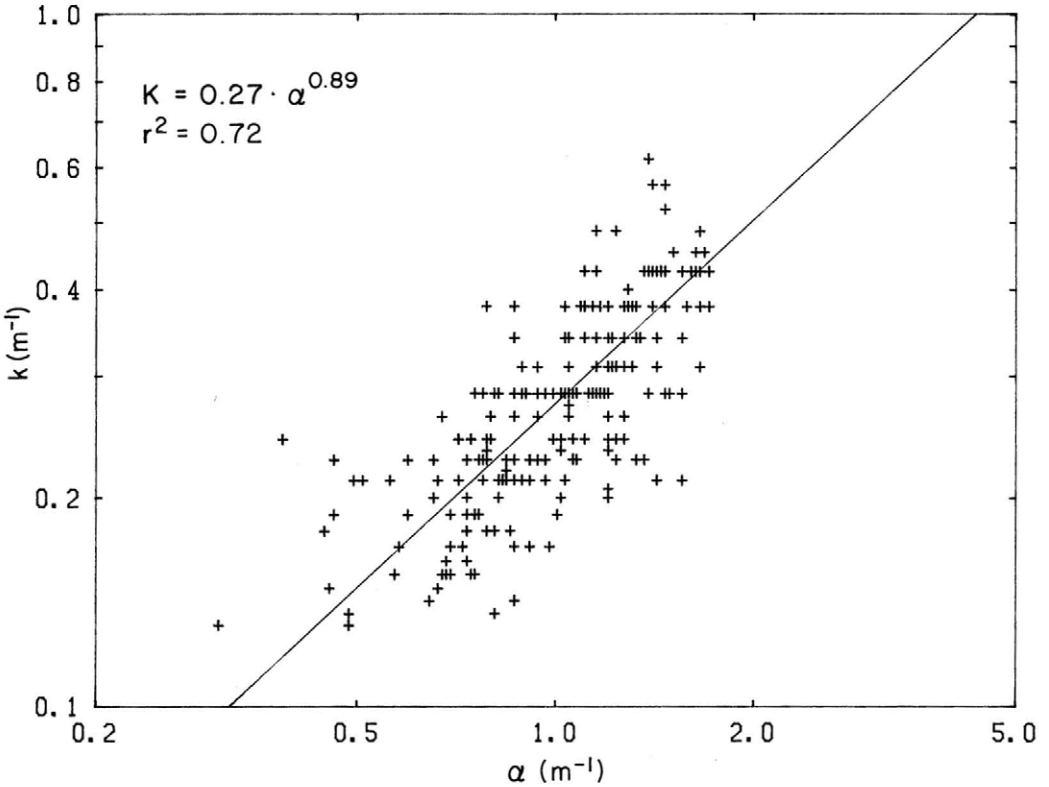


FIGURE 28. Attenuation coefficient (α) versus extinction coefficient (k).

ship is adequate for our data, as determined for Kaneohe Bay by comparing Secchi depth measurements with light intensity profiles taken with a Lambda Model LI-185 quantum radiometer. k was calculated from the radiometer reading as:

$$k = \frac{1}{z} \ln I_o / I_z \qquad (2)$$

where z is the depth at the bottom of the radiometer profile, I_o is the light reading just below the water surface, and I_z is the light reading at the bottom of the profile. Figure 27 demonstrates that equation (1) adequately describes our data.

Measurements of percent transmission (T) with the light transmissometer were converted to beam attenuation coefficients (α) by the relationship:

$$\alpha = -\ln(T/100) \qquad (3)$$

where T is the percent light transmission through a one-meter path. The attenuation coefficients were then empirically related to the extinction coefficients (Figure 28).

The major contribution to the curvilinear relationship of k and α at high extinction coefficients came from the OF station, when stratification of density and particulate and dissolved materials (see Kimmerer, Walsh, and Hirota 1981; also Bay Flushing) lessened the validity of the depth-averaged computations employed to derive these coefficients.

Figure 29 shows the time trend of extinction coefficients at the four stations, with attenuation coefficients converted to extinction coefficients by the relationship shown in Figure 27. Means, 95-percent confidence limits, and percent change with diversion are presented in Table 12. For comparison, filtered bay water was found to have an extinc-

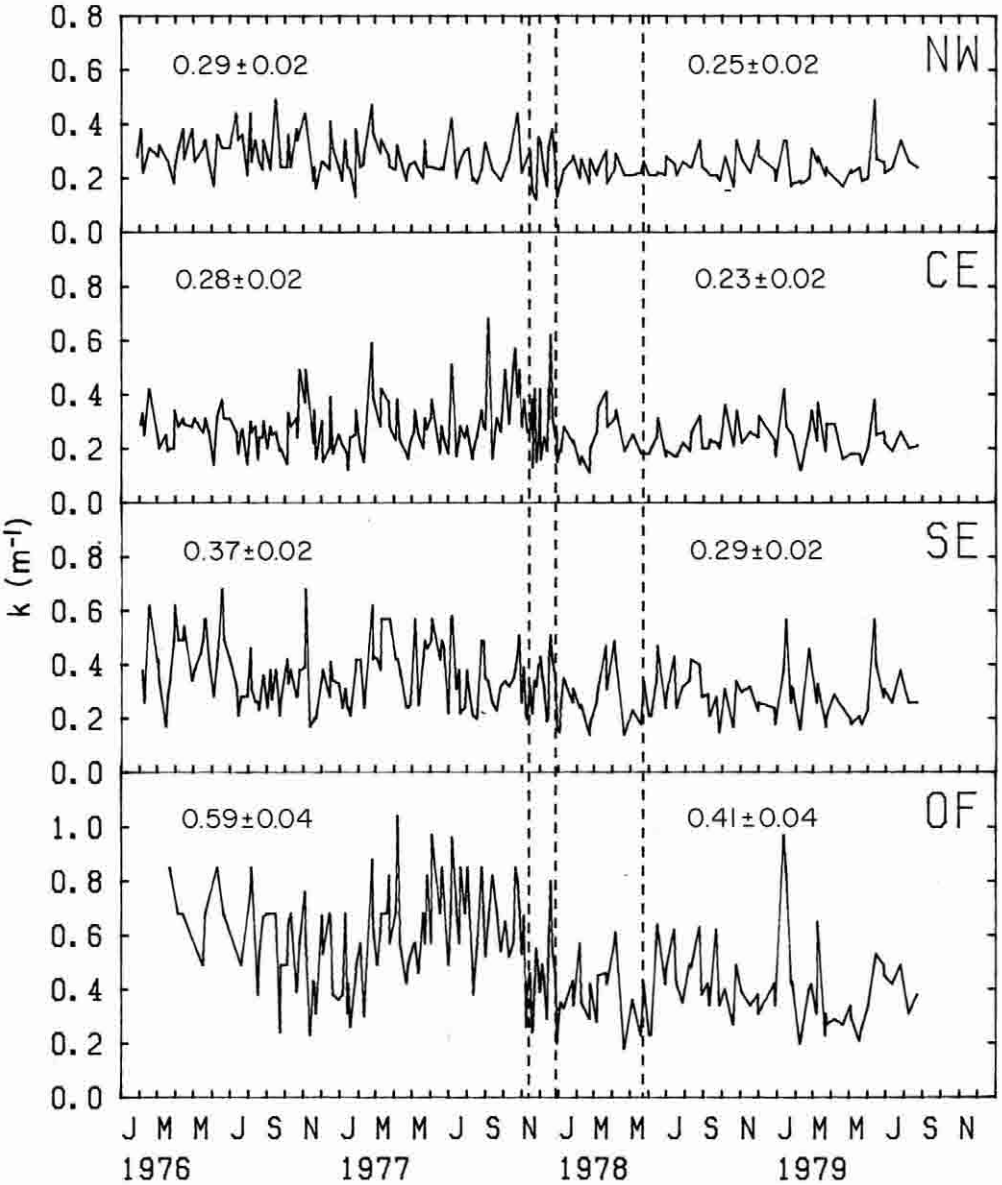


FIGURE 29. Extinction coefficient in the four bay sectors: mean ±95-percent confidence limits of the mean. Vertical dashed lines as in Figure 10.

tion coefficient of 0.07 m^{-1} ($\alpha = 0.22$, $D = 24$), about the same as adjacent oceanic waters ($k = 0.06$, $\alpha = 0.19$, $D = 28$). The clearest water encountered in the bay during our investigation had an extinction coefficient of 0.11 ($\alpha = 0.37$, $D = 15$). This value for D approximates the maximum depth in the bay and was obtained from transmissometer data.

In the open ocean, water clarity is related primarily to chlorophyll (see, e.g., Kiefer and Austin 1974). In coastal settings other particulate materials may also contribute substantially to loss of water clarity. Figure

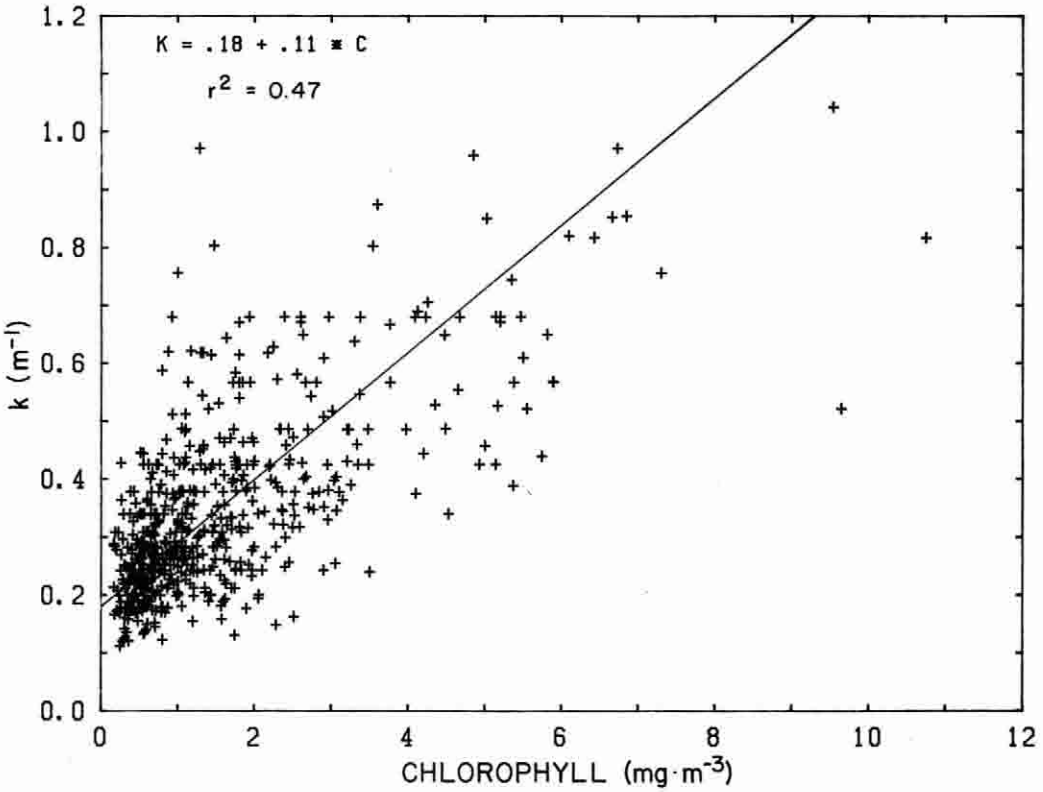


FIGURE 30. Chlorophyll versus extinction coefficient.

30 relates extinction coefficients to chlorophyll data for the bay. The coefficient of determination (0.47) can be compared with values above 0.95 for open-ocean water (Kiefer and Austin 1974). A higher correlation ($r^2 = 0.70$) is obtained for Kaneohe Bay data if extinction coefficients are compared directly with the concentration of particles in the water (Figure 31). Obviously, particles not correlated with chlorophyll contribute substantially to the varying water clarity.

Resuspension of particles by wind mixing is a readily observable phenomenon in Kaneohe Bay. We performed multiple linear regression analyses of the extinction coefficients against the environmental factors defined in the Appendix. The short-term wind speed factors accounted for the greatest proportion of variance in water clarity, and the long-term wind factor was the only other significant item. While runoff during heavy rains can be observed to deliver large amounts of sediments to the bay, at times dramatically decreasing water clarity, the effect did not account for a statistically significant part of the variation in water clarity during our study period.

An analysis of covariance using dates as repeated measures (after Winer 1971) was performed to compare the effect of short-term wind and sewage diversion on attenuation coefficients (Table 13). The short-term wind factor accounted for 25 percent of the between-date component of variance, whereas the diversion accounted for only 14 percent. The interaction term of Table 13 demonstrates that the diversion had quite different effects from one station to another. Table 12 demonstrates that most of the response to sewage diversion occurred at the OF station.

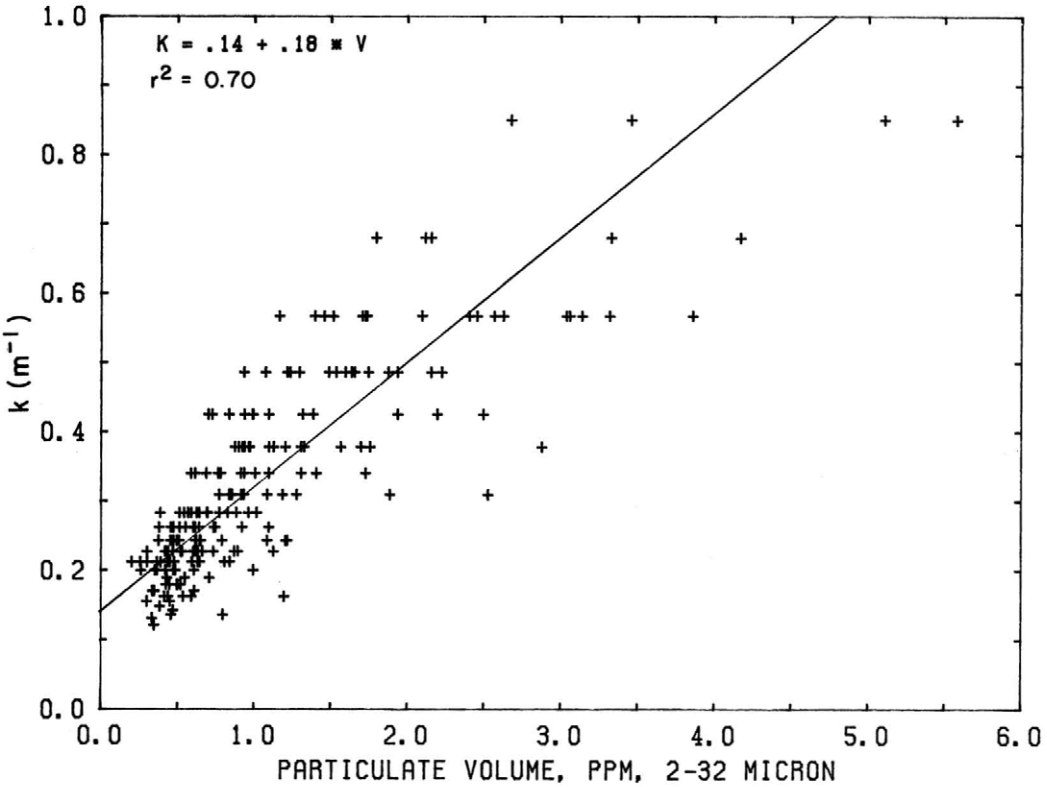


FIGURE 31. Concentration of particulate materials versus extinction coefficient.

TABLE 13

ANALYSIS OF COVARIANCE WITH REPEATED MEASURES OF ALPHA AT ALL FOUR STATIONS VERSUS WIND SPEED, PRE- AND POSTDIVERSION

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	*F*	*P*	PROPORTION OF VARIANCE ACCOUNTED FOR
Between dates						
diversion	15.28	1	15.28	33.86	0.0001	0.14
wind speed factor	26.72	1	26.72	59.20	0.0001	0.25
error	64.99	144	0.45			
Within dates						
stations	117.38	3	39.13	233.78	0.0001	0.56
stations × diversion	17.97	3	5.99	35.80	0.0001	0.09
error	72.80	435	0.17			

The relation between short-term wind mixing and water clarity is graphically illustrated by the detail of vertical distribution of extinction under a variety of wind regimes over several days (Figure 32). Low wind results in particle settling and a relatively thick, high-turbidity, near-bottom nepheloid layer. In the presence of sufficient wind, the water becomes more homogeneous, and the near-bottom nepheloid layer is thinner.

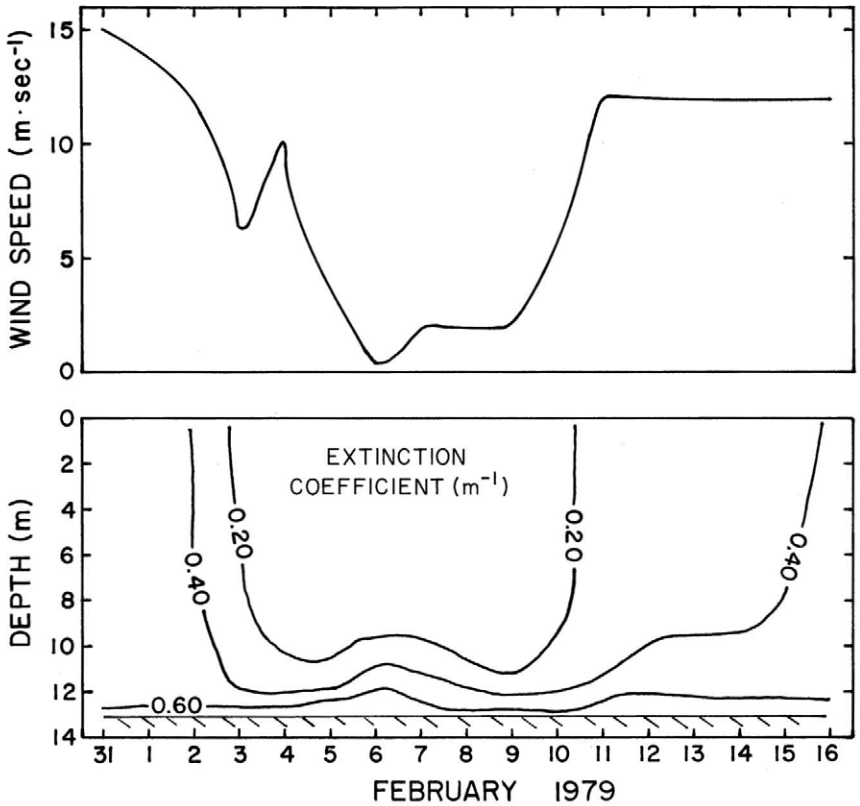


FIGURE 32. Relationship between extinction coefficient throughout the water column at station SE and windspeed over a 17-day period in early 1979.

Numerous measurements of water clarity in Kaneohe Bay have been made over the past two decades. Because of the short-term effects (as illustrated in Figure 32), measurements made infrequently are of little use in understanding long-term trends of water clarity, even though that variable is inherently interesting. Secchi disc data are available for much of 1955 (Doty 1956) and for a one-year period in 1963–1964 (Piyakarnchana 1965). Doty's data yield a mean k of 0.33 in the CE sector. Piyakarnchana's data give a k of 0.27 in 1963 and 0.35 in 1964 in the SE sector; and 0.40 in 1963 and 0.53 in 1964 near our OF station. Comparison of these data with Figure 29 suggests that the change in water clarity from presewage levels to prediversion levels occurred largely in the first year of sewage discharge into the OF sector and that within the first year after sewage diversion values had returned to near presewage levels.

It has been previously demonstrated (Figure 30) that chlorophyll is a significant component of water clarity; this variable is closely related to the delivery of nutrients to support phytoplankton. None of the environmental variables had a strong effect on chlorophyll, although long-term wind speed had a significant effect at station NW; there was also a statistically significant but relatively small annual cycle at stations CE and SE (17% and 14% of the variance, respectively). Analysis of covariance using long-term wind as a covariate demonstrates that diversion was the major component of change in chlorophyll (Table 14); most of that effect was at OF (Table 11). Thus, the observed short-term variation in water clarity largely reflects the addition of inorganic or refrac-

TABLE 14

ANALYSIS OF COVARIANCE USING REPEATED MEASURES ON CHLOROPHYLL, WITH THE LONG-TERM WIND FACTOR AS COVARIATE

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARES	F	P	PROPORTION OF VARIANCE ACCOUNTED FOR
Between dates						
diversion	77.03	1	77.03	46.78	0.0001	0.31
wind-speed factor	0.82	1	0.82	0.50	0.48	—
error	169.61	103	1.65			
Within dates						
stations	344.11	3	114.70	91.49	0.0001	0.39
stations × diversion	153.00	3	50.99	40.68	0.0001	0.17
error	391.17	312	1.25			

tory organic materials to the water column via resuspension or runoff, whereas the longer-term variation in water clarity largely reflects the ability of the ecosystem to sustain a plankton standing crop via the addition of nutrients.

Net chlorophyll (> 35 μm) was determined on aliquots of zooplankton samples. This size fraction represented about 5 percent of total chlorophyll before sewage diversion at stations NW and CE, and at all stations after sewage diversion (Table 15). The contribution of net to total chlorophyll was significantly elevated before sewage diversion at OF and, to a lesser extent, SE. This elevation represents an increase in relative abundance of large phytoplankton near the outfall.

Sediment Composition

Aspects of physiography and sediment composition are directly relevant to the responses of Kaneohe Bay to sewage diversion. Benthic organisms are constrained by the substratum and by the water depth of that substratum. Moreover, the sediments act as a storage reservoir of nutrient material (both particulate and dissolved) which exchanges with the water column. This section provides a basis for later discussion of these separate roles of sediment in the system. Our own sediment analyses are relatively restricted, and we rely heavily on more extensive studies. These include the analyses of Kaneohe Bay as a sedimentary system, as reported by Hollett (1977); MacKenzie et al. (1981); Ristvet (1978); Roy (1970); and Smith, Chave, and Kam (1973).

PHYSIOGRAPHY AND SUBSTRATUM: As shown by Figures 3 and 4 and by Table 2, the bay may be divided into shallow reef flats and a deep lagoon, with intermediate reef slopes. The margin between the reef flats and slopes is distinctive and is here termed the reef crest. Within these categories, a readily observable field discrimination of the substratum types consists of solid substratum within the inner bay (predominantly dead reef limestone), rubble (largely reef limestone rubble, but locally basalt), soft substratum (mixed calcareous and noncalcareous sand, silt, and clay), live coral, and algae (growing on, and often obscuring, solid substratum or rubble).

It has been further demonstrated by grain-size analyses that the soft sediments of the reef flats are largely sand or muddy sand, whereas the reef slope and lagoon floor soft substrata are dominated by mud (i.e., silt and clay).

We have measured the percentage of each substratum type along the benthos sampling transects in each of the sectors (see Biotic Composition) and have used the sector area data of Table 2 to estimate area in the bay by physiographic zone and by substratum type (Table 16).

About 60 percent of the bay is covered by

TABLE 15

MEAN NET CHLOROPHYLL BEFORE AND AFTER SEWAGE DIVERSION
(> 35 μm)

	PREDIVERSION			POSTDIVERSION		
STATION	MEAN $mg \cdot m^{-3}$	95% CONFIDENCE LIMITS OF MEAN	PERCENT OF MEAN TOTAL CHLOROPHYLL	MEAN $mg \cdot m^{-3}$	95% CONFIDENCE LIMITS OF MEAN	PERCENT OF MEAN TOTAL CHLOROPHYLL
NW	0.035 ± 0.01		5	0.027 ± 0.009		5
CE	0.045 ± 0.02		5	0.03 ± 0.02		5
SE	0.150 ± 0.04		8	0.06 ± 0.02		5
OF	0.58 ± 0.19		12	0.08 ± 0.03		6

TABLE 16

SUMMARY OF AREAS IN EACH PHYSIOGRAPHIC ZONE, SHOWING PERCENTAGE OF EACH ZONE WITHIN A SECTOR, AND PERCENTAGE OF SUBSTRATUM TYPES WITHIN EACH ZONE

SECTOR & ZONE	AREA		SUBSTRATUM TYPE (PERCENT OF ZONE AREA)					
	($10^6 m^2$)	%	SOLID	RUBBLE	ALGAE	CORAL	SANDY	MUDDY
NW								
lagoon	3.5	32	0	0	0	0	0	100
slope	1.8	17	6	1	4	17	0	73
crest*	0.3	3	47	3	0	1	49	0
flat	5.2	48	1	12	16	0	71	0
total	10.8	100	3	6	8	3	36	44
CE								
lagoon	7.2	59	0	0	0	0	0	100
slope	1.7	14	2	30	24	1	0	42
crest*	0.2	1	44	12	24	20	0	0
flat	3.2	26	10	12	20	3	55	0
total	12.3	100	4	7	9	1	14	64
SE/OF								
lagoon	4.2	51	0	0	0	0	0	100
slope	2.6	30	16	16	0	0	0	68
crest*	0.1	1	28	24	0	2	45	0
flat	1.5	18	3	40	4	0	53	0
total	8.4	100	6	12	1	0	10	71
TOTAL								
lagoon	14.9	47	0	0	0	0	0	100
slope	6.0	19	9	16	8	6	0	62
crest*	0.5	2	43	9	8	6	34	0
flat	10.0	32	4	16	15	1	63	0
total	31.0	100	4	8	6	2	20	59

*Crest is figured as 5% of reef flat.

mud, which is largely confined to the lagoon floor. Sand, which covers 20 percent of the bay area, is primarily found on the reef flats. Rubble covers 8 percent of the bay area, largely on the reef flats and crests, and algae (predominantly growing on and obscuring rubble on the reef flats) cover 6 percent of the area. Solid substratum and live coral are uncommon substratum types in the inner bay, although both are important in the outer bay.

There are some conspicuous differences

TABLE 17

PARTICULATE ORGANIC CARBON, NITROGEN, AND PHOSPHORUS IN UPPER 10 cm OF LAGOON SEDIMENTS

		CARBON			NITROGEN			PHOSPHORUS		
	MUD-BOTTOM AREA ($10^6 m^2$)	MEAN % BY WEIGHT	± 95%	N	MEAN % BY WEIGHT	± 95%	N	MEAN % BY WEIGHT	± 95%	N
NW	4.81	3.3	± 0.3	30	0.19	± 0.02	42	0.077	± 0.009	3
CE	7.91	2.9	± 0.5	22	0.20	± 0.02	33	0.077	± 0.012	2
SE/OF	5.98	2.7	± 0.3	17	0.16	± 0.02	30	0.119	± 0.028	2
Entire bay	18.70	2.9			0.18			0.09		

TABLE 18

CONCENTRATION OF DISSOLVED INORGANIC NUTRIENTS IN UPPER 30 cm OF LAGOON SEDIMENTS ($mmoles \cdot m^{-3}$)

	AREA MUD-BOTTOM ($10^6 m^2$)	NH_4		NO_3		PO_4		Si*
		MEAN ± 95%	N	MEAN ± 95%	N	MEAN ± 95%	N	MEAN
NW	4.81	83 ± 27	11	5 ± 2	8	16 ± 4	8	—
CE	7.91	142 ± 59	9	4 ± 5	9	9 ± 5	10	—
SE/OF	5.98	262 ± 27	94	4 ± 2	106	24 ± 7	105	—
Bay average	18.70	165		4		16		310

*From MacKenzie et al. (1981).

between sectors in physiography and substratum type. The NW sector has a low proportion of lagoon and a correspondingly low amount of mud. The SE sector has a large area assigned to the slope category relative to the reef flats, reflecting in part extensive dredging of reef flats to intermediate depths (3–6 m). Solid substratum and rubble from dead reefs are more abundant in the SE sector than elsewhere, and coral cover is lower there.

CHEMICAL COMPOSITION: Various aspects of sediment chemistry have been extensively investigated in Kaneohe Bay (Hollett 1977; MacKenzie et al. 1981; Ristvet 1978; Smith, Chave, and Kam 1973). Of most direct relevance to the present investigation is the role of sediments in storing and cycling nutrients within the ecosystem. We have therefore characterized the particulate and dissolved nutrient composition of the lagoon sediments in the bay. Reef flat sediment chemistry is not discussed, because we concluded that the relatively thin loose sediment veneer of the reef flat was not quantitatively as important in nutrient storage and cycling as the thicker and areally more extensive sediment of the lagoon.

Table 17 summarizes the particulate organic carbon, nitrogen, and phosphorus content of lagoon sediments. Phosphorus data are very limited, because we developed a technique which we found to be satisfactory for particulate phosphorus only very late in the program. The analyses reported here are based on grab samples of the upper 10 cm of sediment. Available information (MacKenzie et al. 1981; Ristvet 1978) reveals no significant vertical trend in the organic content of cores from the bay, to a depth of at least 150 cm. The data in Table 17 also fail to reveal any significant differences between sectors in particulate organic content of lagoon sediments. This observation is consistent with data presented by Hollett (1977).

In Table 18 we present data on dissolved inorganic nutrients from sediment cores 30

TABLE 19

RESERVOIR SIZE OF NUTRIENTS IN KANEOHE BAY LAGOON SEDIMENTS
(kmoles)

	NW	CE	SE/OF	BAY TOTAL
Mud-bottom area ($10^6 m^2$)	4.81	7.91	5.98	18.70
Nitrogen				
particulate	1.5×10^5	2.5×10^5	1.5×10^5	5.5×10^5
dissolved	96	261	354	211
Phosphorus				
particulate	2.7×10^4	4.4×10^4	5.2×10^4	12.3×10^4
dissolved	17	16	32	65
Dissolved Silicon	330	550	420	1300
Particulate Carbon	3.0×10^6	4.3×10^6	3.0×10^6	10.3×10^6

NOTE: Assumes sediment density of 3 $g \cdot cm^{-3}$, 75 percent porosity, and sediment reservoir 30 cm thick.

cm in length. Ammonium is the dominant form of dissolved inorganic nitrogen in the sediments and apparently increases from the NW sector toward the SE. An insignificant amount of nitrate is present. Phosphate shows no significant difference among locations. Our own data for silicon in interstitial waters are unreliable, but data by MacKenzie et al. (in press) give a mean silicon content of 310 mmoles $\cdot m^{-3}$, with no significant variation with depth in the cores or with location in the bay.

With some assumptions about the amount of sediment that interacts with the overlying water column, we can estimate the approximate magnitude of the sediment nutrient reservoir. Our own observations (see Metabolism; also Harrison 1981) and information in Ristvet (1978) suggest that the sediments are actively reworked by burrowing organisms to a depth of about 30–40 cm (we use 30 cm here). We assume that this zone of biological mixing, or "bioturbation," marks the limit of significant sediment interaction with the water column.

Roy (1970) estimated the lagoon sedimentation rate to be at least 3.9 $cm \cdot yr^{-1}$ in the previous four decades, and Hollett (1977) did not significantly modify this estimate. Thus, the upper 30 cm of sediment represent only about eight years' accumulation of materials—substantially less time than the period of sewage discharge (Figure 5).

Table 19 presents the results of these rough reservoir calculations. Clearly the particulate nutrient pools far exceed the dissolved pools of the sediments. The particulate nitrogen and phosphorus in the upper 30 cm of the lagoonal sediment column far exceed total nutrient loading over the past decade (Table 7). This particulate accumulation must be largely derived from stream runoff in excess of the estimated runoff (see also Hydrology).

Bay sediments contain an average by weight of about 60 percent $CaCO_3$, which originates in the bay; most of the remaining 40 percent of the sediment is land-derived inorganic materials (Smith, Chave, and Kam 1973). In the Hydrology section we stated that streams contain about 4 percent organic carbon in their suspended-load fraction. Diluting that 4 percent by 60 percent with locally produced $CaCO_3$ containing no organic carbon would yield a sediment with 1.6 percent organic carbon—over half the observed percentage. Because the organic carbon stays relatively constant with depth in the sediments, we can assume that this particulate reservoir is largely refractory and is not highly interactive in ongoing benthic biochemical processes. This point will be discussed further in the section on Metabolism.

By contrast, the dissolved nutrient reservoirs in the upper 30 cm of the sediment column are equivalent to only a few days of nutrient loading (compare Tables 7 and 19).

TABLE 20

VARIABLES RELATED TO PHYTOPLANKTON PLUS MICROHETEROTROPH BIOMASS ($mg \cdot m^{-3}$)

SECTOR AND VOLUME ($10^6 m^3$)	NW 66.41 MEAN ± 95%	N	CE 119.68 MEAN ± 95%	N	SE 74.24 MEAN ± 95%	N	OF 5.35 MEAN ± 95%	N	BAY AVERAGE 265.68	OCEAN*
Chlorophyll										
pre	0.61 ± 0.10	44	0.71 ± 0.10	44	1.78 ± 0.21	50	4.40 ± 0.25	25	1.06	0.20
post	0.52 ± 0.12	26	0.53 ± 0.12	26	1.08 ± 0.23	26	1.38 ± 0.27	26	0.70	
ATP										
pre	0.13 ± 0.04	9	0.20 ± 0.04	9	0.43 ± 0.21	14	1.00 ± 0.37	14	0.26	< 0.07
post	0.07 ± 0.01	17	0.11 ± 0.06	18	0.25 ± 0.11	18	0.25 ± 0.08	17	0.14	
Particulate Organic Carbon										
pre	181 ± 27	43	183 ± 34	43	260 ± 28	49	400 ± 53	34	208	47
post	150 ± 24	26	137 ± 22	26	192 ± 30	26	207 ± 31	26	157	

*Oceanic chlorophyll and particulate organic carbon from Laws (1980); oceanic ATP assumed to be lower than lowest bay sector mean values, although no data available.

The exact size of this reservoir is obviously sensitive to the depth chosen as the base of the interactive sediments. Data presented by MacKenzie et al. (1981) indicate that ammonium and phosphate increase with depth in the core, whereas nitrate and dissolved silicon do not. This increase suggests that some long-term oxidation process does slowly use a small fraction of the particulate organic materials. The nonrefractory fraction that is used appears to be a very small portion of the total particulate organic reservoir.

Biotic Composition

Of particular interest in the response of the ecosystem to sewage diversion is the biotic composition and the changes in composition both spatially and temporally. We have, for the most part, concentrated our efforts on total biomass and on the more functional aspects of the biota. Because of the different operational procedures and personnel involved in the biological studies, it is convenient to consider the biota in the following categories: Phytoplankton and microheterotrophs, zooplankton, benthic algae, and benthic animals including reef fishes.

The nekton (other than reef fishes) were not directly addressed in this study for two primary reasons. First, the major nektonic organism in the bay is the anchovy *Stolephorus purpureus* (Hawaiian *nehu*); the population biology of this fish has been the subject of an ongoing doctoral dissertation (T. Cooney, in preparation). We have collected incidental information in the form of date on *nehu* eggs and larval abundances. Second, the nekton other than reef fishes make up a relatively small proportion of the bay biomass, and we judged the effort required to study this biotic component too large for the information we were likely to gain.

Methods used in the biological sampling are presented in the Appendix.

PHYTOPLANKTON AND MICROHETEROTROPHS: Studies of the phytoplankton and microheterotroph biomass in bay waters consisted of measuring the standing crop of chlorophyll, ATP, particulate organic carbon and nitrogen, and nutrients. The particulate materials analyzed were those particles that passed through a 102-μm-mesh screen. In addition, ^{14}C productivity was measured in the water column, and both depth-integrated and maximum-productivity indices (^{14}C : chlorophyll) were estimated. Many of these data have been reported in the section on Water Composition; here we concentrate on those variables not explicitly covered elsewhere.

Table 20 presents data related to phytoplankton and microheterotroph biomass. The chlorophyll and particulate organic carbon data differ slightly from those presented in Table 11, because the present data set is restricted to stations at which ^{14}C productivity was measured (Phytoplankton Metabolism). Phytoplankton biomass ($mgC \cdot m^{-3}$) can be estimated as 50 times the chlorophyll standing crop (Caperon, Harvey, and Steinhilper 1976; Strickland and Parsons 1972), and living organic carbon as 310 times the ATP (Holm-Hansen 1970; Hunter 1978). Because these figures change with the nutritional state of the organisms in question, they must be taken as no more than rough indices of biomass. Detrital carbon is calculable as particulate organic carbon minus the estimates of living carbon. Microheterotrophic living carbon is living carbon minus carbon associated with chlorophyll. These calculations are clearly imperfect approximations, but they provide our best present ability to evaluate the standing crop of detritus, microheterotrophs, and phytoplankton in the water column. Table 21 summarizes the results.

The total amount of particulate carbon decreased with distance from the outfall and decreased with sewage diversion, as previously discussed. Detrital carbon varied only slightly, either with location or with sewage diversion, so that the change in particulate carbon has involved the living carbon almost exclusively. The bay-wide average of living carbon dropped from 81 to 44 $mgC \cdot m^{-3}$; the drop is most dramatic at the OF station. The microheterotrophs showed a proportionally larger spatial gra-

TABLE 21

ESTIMATES OF PHYTOPLANKTON CARBON, MICROHETEROTROPH CARBON, DETRITAL ORGANIC CARBON, AND PARTICULATE ORGANIC CARBON, ACCORDING TO ASSUMPTIONS IN TEXT

	NW		CE		SE		OF		BAY AVERAGE		
	PRE	POST	PRE	POST	PRE	POST	PRE	POST	PRE	POST	OCEAN
Particulate standing crop ($mg \cdot m^{-3}$)											
Phytoplankton	31	26	36	27	89	54	220	69	53	35	10
Microheterotroph	9	(−4)*	26	7	44	24	90	9	28	9	~10
Total Living	40	22	62	34	133	78	310	78	81	44	~20
Detritus	141	128	121	103	127	114	90	129	127	113	~27
Total	181	150	183	137	260	192	400	207	208	157	47
Phytoplankton as % of living	78	(100)*	58	79	67	69	71	88	64	80	~50
Phytoplankton as % of total	17	17	20	20	34	28	55	33	25	22	21
Detritus as % of total	78	85	66	75	49	59	23	62	61	72	~57

*Total living carbon exceeded phytoplankton carbon as evaluated, resulting in negative microheterotroph carbon.

TABLE 22

SUMMARY STATISTICS FOR ZOOPLANKTON BIOMASS DATA ($mg \cdot m^{-3}$)

	NW		CE		SE		OF	
	MEAN ± 95%	N	MEAN ± 95%	N	MEAN ± 95%	N	MEAN ± 95%	N
Macroplankton dry weight								
pre	14.6 ± 5.2	41	43 ± 12	41	98 ± 17	41	107 ± 24	39
post	16.8 ± 6.8	37	31 ± 8	37	64 ± 12	37	70 ± 16	37
Neuston dry weight								
pre	9.4 ± 3.4	41	29.0 ± 8.7	41	55 ± 12	41	59 ± 15	37
post	11.5 ± 3.6	36	30.8 ± 4.8	37	41 ± 12	37	45 ± 18	37
Microplankton dry weight								
pre	250 ± 70	41	128 ± 17	41	215 ± 24	41	412 ± 56	39
post	212 ± 63	37	100 ± 17	37	136 ± 19	37	196 ± 33	37
Microplankton ash-free dry weight								
pre	55 ± 11	41	72 ± 9.4	41	120 ± 14	40	216 ± 30	39
post	58 ± 26	36	53 ± 7.1	36	80 ± 12	36	107 ± 17	36
Net chlorophyll								
pre	0.034 ± .012	41	0.045 ± .025	41	0.154 ± .040	40	0.570 ± .190	39
post	0.027 ± .009	37	0.032 ± .017	37	0.059 ± .022	37	0.075 ± .030	37

dient and a larger proportional drop, even though the phytoplankton dominate the biomass.

The variation in this fraction of particulate materials in the water column may be summarized as follows. In terms of relative abundance, detritus dominates and phytoplankton are next. The abundance of phytoplankton was a function of the average nutrient input. Both before and after sewage diversion, all of these carbon fractions were elevated substantially above oceanic values.

It is also useful, for comparison with other biomass components, to calculate the phyto-

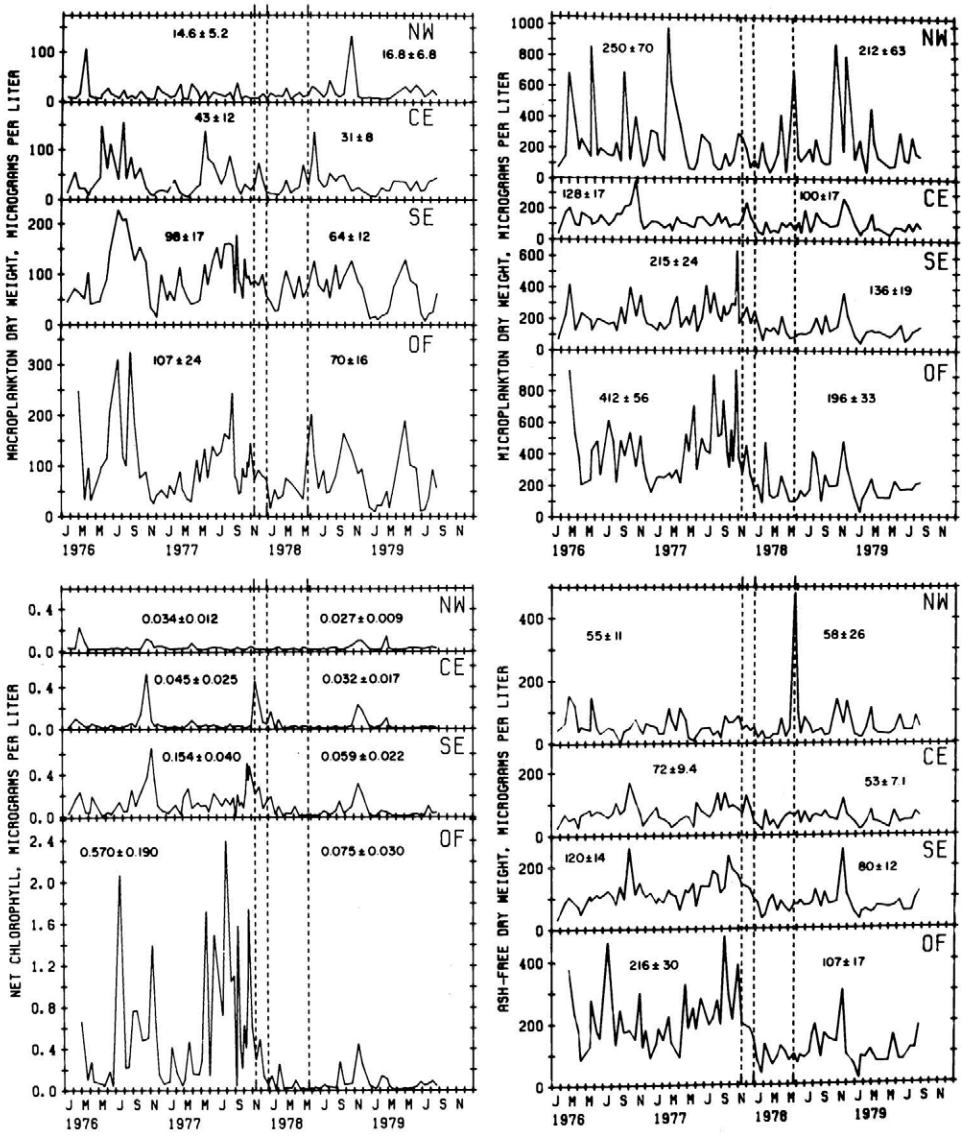


FIGURE 33. Various measures of zooplankton biomass, mean ±95-percent confidence limits of the mean. Vertical dashed lines as in Figure 10.

plankton and microheterotroph biomass in the bay. Phytoplankton biomass totalled about 14 tons of carbon before sewage diversion and dropped to about 9 after. Microheterotroph carbon dropped from 7 to 3 tons. The Redfield C : N : P ratio (106 : 16 : 1) can be used to estimate the phytoplankton and microheterotroph nutrient standing crop for eventual comparison with changing nutrient loading (Ecosystem Dynamics). The phytoplankton biomass before sewage diversion was equivalent to about 177 and 11 kmoles nitrogen and phosphorus, respectively, and dropped to 117 and 7 kmoles nitrogen and phosphorus, respectively, after diversion. The microheterotrophs dropped from a ni-

TABLE 23

ANALYSIS OF COVARIANCE USING REPEATED MEASURES OF LOG-TRANSFORMED DATA

	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	P	PROPORTION OF VARIANCE ACCOUNTED FOR
Macroplankton dry weight						
Between dates						
diversion	4.42	1	4.42	5.16	.026	.04
annual cycle	34.52	2	17.26	20.15	< .001	.35
error	61.68	72	0.86			
Within dates						
stations	167.16	3	55.72	171.38	< .001	.68
stations × diversion	4.89	3	1.63	5.01	.002	.02
error	72.18	222	0.32			
Microplankton ash-free dry weight						
Between dates						
diversion	13.48	1	13.84	44.99	< .001	.30
annual cycle	7.51	2	3.75	12.10	< .001	.16
long-term wind factor	3.32	1	3.32	10.78	.002	.07
error	21.22	69	0.31			
Within dates						
stations	63.62	3	21.21	128.14	< .001	.62
stations × diversion	2.63	3	0.88	5.29	.002	.02
error	35.75	216	0.17			

NOTE: The covariate is the sum of an annual sine and cosine function.

trogen and phosphorus standing crop of 93 and 6 kmoles, respectively, to 31 and 2 kmoles.

Both available data (Figure 26) and comments in the literature (Tester 1951) indicate that the bay waters have historically had somewhat elevated levels of particulate materials, including phytoplankton (inferred from chlorophyll), even before sewage discharge began. From the limited early observations, we conclude that since sewage diversion the phytoplankton and microheterotroph nutrient standing crops have dropped to approximately presewage levels, although they still remain above oceanic levels.

ZOOPLANKTON: Table 22 presents means, 95 percent confidence limits, and numbers of samples for several measures of zooplankton biomass at each station for the prediversion and postdiversion sampling periods. All measures of biomass decreased with sewage diversion at all but station NW, with the greatest decrease occurring in the southern basin (SE and OF). The general trend of biomass, both before and after sewage diversion, was an increase in biomass from NW to OF. An exception is microplankton dry weight, which was very high at NW. A large fraction of the microplankton dry weight is suspended inorganic matter, so we will use ash-free dry weight as the biomass measure for this size fraction.

Figure 33 shows the time trends at all four stations of macroplankton dry weight and microplankton dry weight, microplankton ash-free dry weight, and chlorophyll. Evidence of a seasonal cycle can be seen most clearly in the macroplankton dry weight and may be present in the other data as well. Because the pre- and postdiversion periods were longer than one year but less than two, they included incomplete portions of the annual cycle. Consequently, this cycle must be corrected for in attempting to detect differences between the two periods. Furthermore, it is possible that the changes in the mean values that occurred at the time of

TABLE 24

ZOOPLANKTON BIOMASS

	NW	CE	SE	OF
Macroplankton dry weight				
pre	10.4	30.0*	83.9*	84.8*
post	12.1	24.5	52.5	53.6
Neuston dry weight				
pre	5.6	18.0*	38.3	40.0
post	7.8	13.6	25.7	25.7
Microplankton dry weight				
pre	191	121*	207*	379*
post	157	89	127	173
Microplankton ash-free dry weight				
pre	47.3	70.0	122.0*	205.8*
post	35.4	46.1	70.4	92.7

NOTE: Cell means, adjusted for significant independent variable (from Table 23) and converted to antilogs. Underlined stations do not differ significantly from one another ($p < 0.01$, Newman-Keuls test).
*Significant differences between pre- and postdiversion.

diversion were a result of coincidental meteorological and hydrological shifts. To examine this possibility, we performed multiple linear regressions of the biomass variables against all combinations of the environmental variables described in the Appendix. The annual cycle, a linear combination of a sine and cosine term, was significant for the zooplankton biomass measures. No other environmental variables had a significant effect beyond that explained by the annual cycle, except for a slight effect of the long-term wind factor on microplankton ash-free dry weight.

To test for differences between pre- and postdiversion periods and among stations, we used analysis of covariance with repeated measures. Log-transformed values were used, because the variances increased with the means (Table 22). Analysis of covariance tables are presented only for macroplankton dry weight and microplankton ash-free dry weight (Table 23); neuston dry weight and net chlorophyll showed similar patterns, respectively. For macroplankton and neuston dry weight the major source of temporal variation was the annual cycle. Microplankton ash-free dry weight and net chlorophyll were mainly responsive to the diversion. All four variables differed significantly among stations, and interaction terms were significant. Table 24 shows adjusted cell means and significance of multiple range tests. For all of the variables there was a general decrease in standing crop from OF station to NW; that gradient was more evident before diversion than afterwards.

Carbon and nitrogen analyses were done for 1976 and 1978 samples (i.e., one prediversion year and one postdiversion year). Table 25 presents summary statistics for carbon and nitrogen for vertical and surface samples at each station for each year. Macroplankton and neuston C : N ratios at all stations were around 4, and microplankton C : N ratios at stations CE, SE, and OF around 5. The values of microplankton C : N of 11 and 13 at station NW indicate a relatively larger detrital contribution.

We estimated the contribution of plant, animal, and detrital carbon to the total microplankton carbon and nitrogen using a method modified from that of Hirota and Szyper (1976). Phytoplankton carbon : chlorophyll and C : N mass ratios are assumed to be 50 : 1 and 4.7 : 1, respectively, and zooplankton C : N ratios are assumed to be 4 : 1. Hirota and Szyper (1976) assumed the detrital C : N ratio to be 8.8 : 1, but application of this value to our data leads to negative numbers for zooplankton carbon, and a median at station NW of 0. The highest total microplankton C : N ratio was 28 : 1; use of this figure gave a mean percentage animal carbon at station NW of 26 percent. This agrees with rough estimates from examination of preserved samples; therefore the detrital C : N ratio was taken to be 28. The results of these calculations are shown in Table 26. The large contribution of phytoplankton, especially before diversion, is evident and consistent with Table 2.2. Progressive increases of estimated zooplankton and phytoplankton carbon and nitrogen from station NW to station OF can be seen, and it is clear that plant and animal carbon and nitrogen are masked in part by the large detrital contribution at NW. This result is also consistent with analysis of samples smaller than 102 μm, as reported in Table

TABLE 25

Numbers of Samples, Means, and 95-percent Confidence Limits for Macroplankton, Microplankton, and Neuston Carbon and Nitrogen

		NW		CE		SE		OF	
		1976*	1978†	1976	1978	1976	1978	1976	1978
Macroplankton	*N*	21	22	21	22	21	22	19	22
Carbon	Mean	4	6	10	8	20	17	26	17
	C.L.	± 8	± 10	±13	± 8	± 20	± 9.5	± 40	± 15
Nitrogen	Mean	1.0	1.5	3	2	5	4	7	4
	C.L.	± 2.2	± 2.8	± 4	± 2	± 5	± 3	± 10	± 4
Microplankton	*N*	21	22	21	22	21	22	19	22
Carbon	Mean	38	55	35	26	53	42	95	48
	C.L.	± 53	± 152	± 27	± 21	± 34	± 30	± 77	± 52
Nitrogen	Mean	3	4	7	5	10	8	17	10
	C.L.	± 3	± 9	± 6	± 4	± 7	± 4	± 11	± 8
Neuston	*N*	20	22	21	21	21	22	17	22
Carbon	Mean	3	4	8	6	13	15	18	11
	C.L.	± 5	± 6	± 17	± 10	± 13	± 10	± 33	± 11
Nitrogen	Mean	0.9	1.0	2	2	3	4	4	3
	C.L.	± 1.3	± 1.4	± 4	± 3	± 4	± 6	± 8	± 3

*Prediversion.
†Postdiversion.

TABLE 26

Mean Microzooplankton Carbon and Nitrogen Values with Estimated Percent Contribution Due to Zooplankton, Phytoplankton (including Chlorophyll Degradation Products), and Detritus

	NW		CE		SE		OF	
	PRE	POST	PRE	POST	PRE	POST	PRE	POST
Carbon ($mg \cdot m^{-3}$)	38.9	45.8	33.8	25.9	52.6	41.1	95.6	46.9
Percentage breakdown:								
zooplankton	24	28	64	71	61	72	55	73
phytoplankton	7	4	9	7	14	9	22	8
detritus	69	67	27	22	25	19	23	19
Nitrogen ($mg \cdot m^{-3}$)	3.2	4.0	6.6	5.2	10.1	8.2	17.8	9.3
Percentage breakdown:								
zooplankton	50	53	82	87	79	85	69	87
phytoplankton	17	12	12	8	16	11	27	9
detritus	33	35	6	5	5	4	4	4

21. Of course the result of this calculation depends heavily upon the assumed C : N ratio of detritus.

Power functions of total carbon and nitrogen versus dry weight for macroplankton and neuston samples, and ash-free dry weight for microplankton, are presented in Table 27. This table is based on individual samples rather than means of duplicate samples as in Table 22; hence the number of samples is higher. Because of the high correlations between both carbon and nitrogen and dry weight, especially for macroplankton and neuston, the carbon and nitrogen

TABLE 27

RELATIONSHIPS OF ZOOPLANKTON CARBON AND NITROGEN TO DRY WEIGHT AND ASH-FREE DRY WEIGHT ($mg \cdot m^{-3}$)

	CARBON	NITROGEN	N	r^2
Macroplankton	$0.346\ DW^{0.886}$	$0.083\ DW^{0.904}$	314	0.96
Neuston	$0.355\ DW^{0.929}$	$0.086\ DW^{0.944}$	206	0.94
Microplankton*	$0.57\ AFDW^{0.974}$	$0.031\ AFDW^{1.223}$	189	0.86(C) 0.74(N)

*One outlier removed.

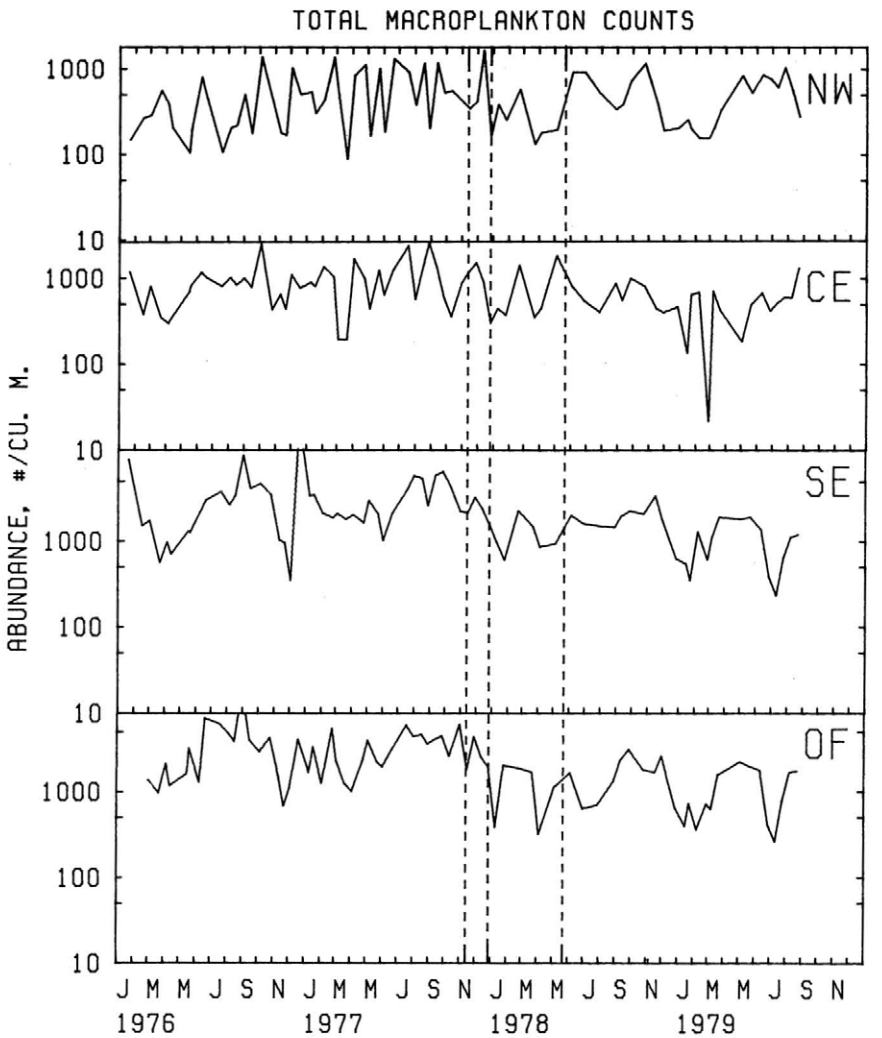


FIGURE 34. Number of total macroplankton per cubic meter in the four sectors. Vertical dashed lines as in Figure 10.

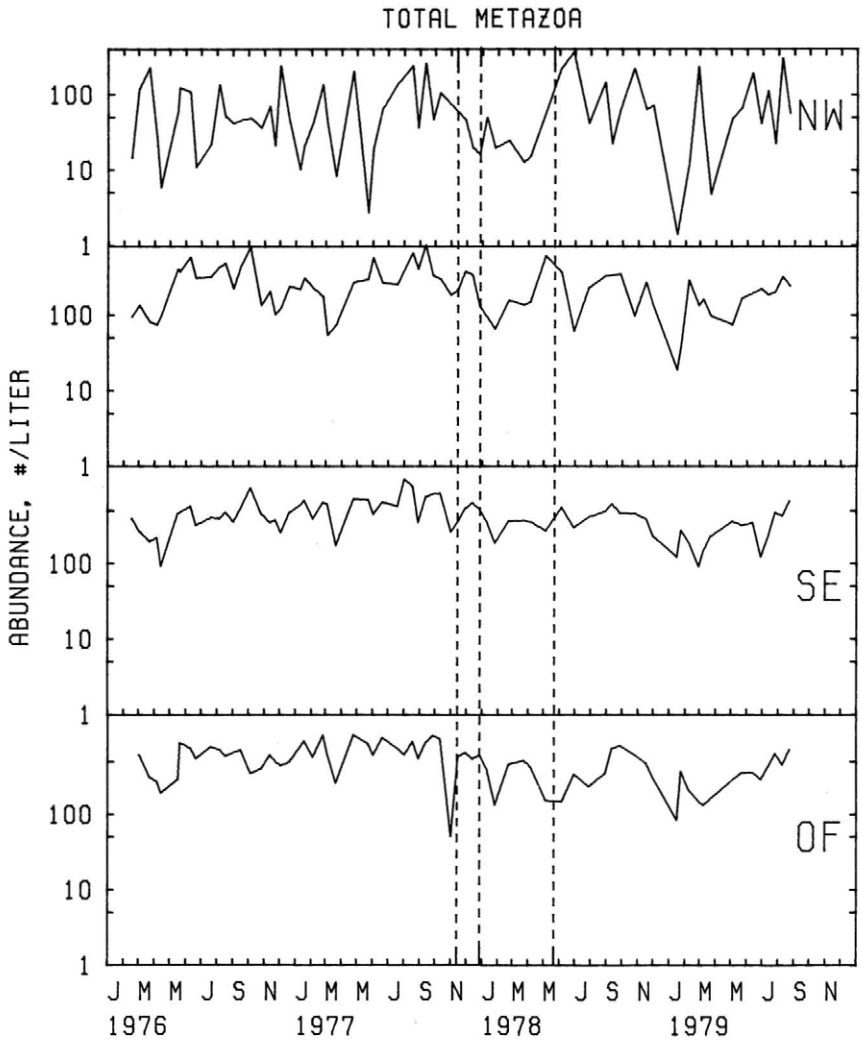


FIGURE 35. Number of total microplanktonic metazoans per cubic meter in the four sectors. Vertical dashed lines as in Figure 10.

values can be expected to follow time trends similar to those in Figure 33, and to have the same relationships between stations, and between pre- and postdiversion, as did the dry weight figures.

Considerable effort was expended on counting zooplankton samples for taxonomic abundances. Since these data will be reported elsewhere (Kimmerer, in preparation), only a brief summary of salient points is presented here.

The zooplankton of Kaneohe Bay have been studied sporadically in the last three decades, and the general patterns of abundance are well known. The greatest numbers of the more common taxa are found in the southern basin, with abundances decreasing toward the north. The plankton community of the southern basin has low diversity, while that in the northern reaches of the bay is in a zone of mixing between two or more communities and has a much higher diversity.

Figures 34 and 35 show the patterns of abundance of total macroplankton counts

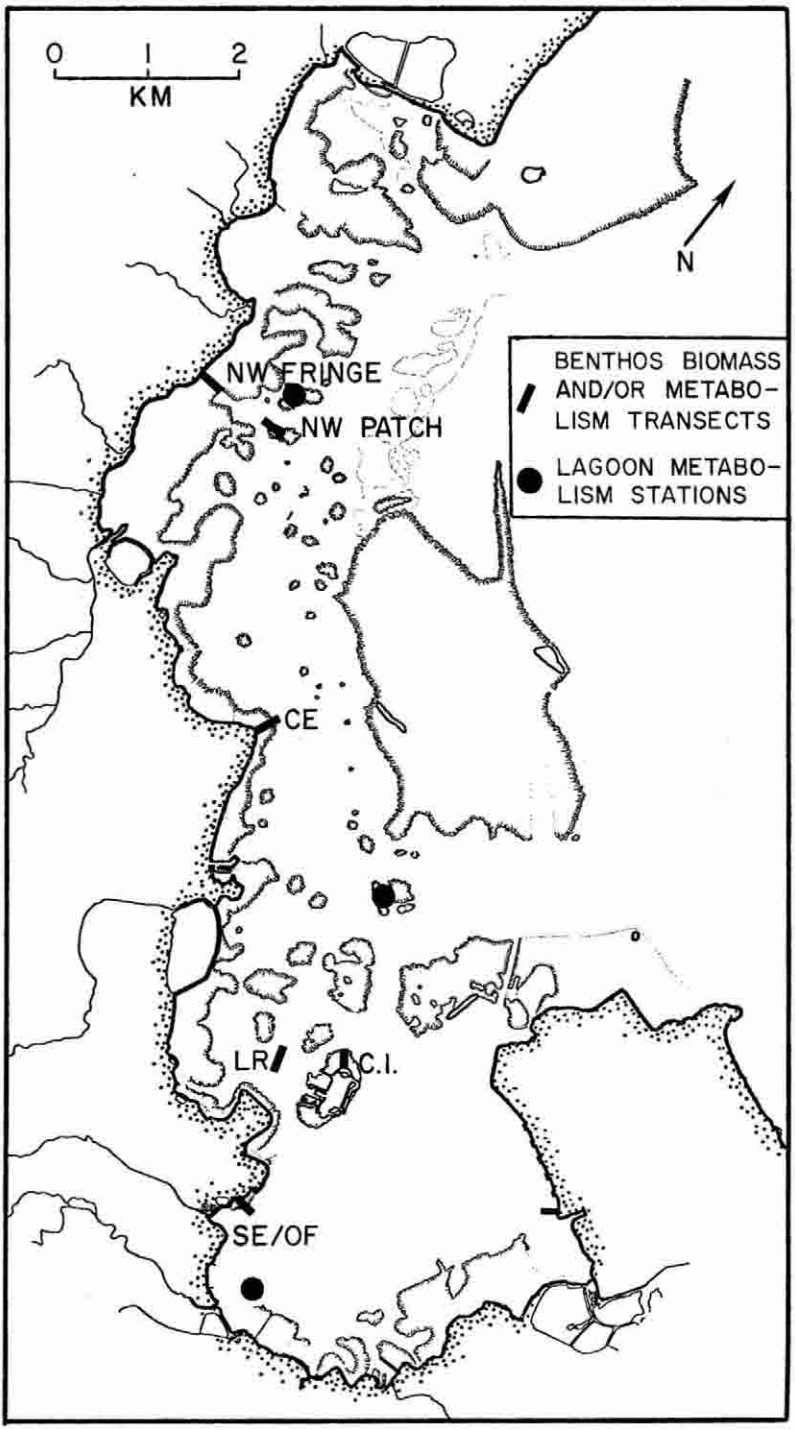


FIGURE 36. Map showing location of the four major transects used for benthic biomass studies (SE, CE, NW Fringe, NW Patch), the additional sites used for reef-flat metabolism studies (CI, LR), and the sites used for lagoon-floor metabolism studies (●).

and total microplankton metazoa, respectively. Note the logarithmic y axes on both figures. The microplankton count data included some very abundant protists, especially tintinnids and presumably heterotrophic dinoflagellates. These were excluded from Figure 35 because of huge fluctuations in their abundances, and because in terms of biomass they were relatively unimportant. It can be seen that both sets of count data followed the same general trends as the biomass data: abundances decreasing from south to north, and decreasing slightly with sewage diversion. Total abundances at stations SE and OF were not different, and were about one order of magnitude higher than at NW.

Plankton community structure can be a powerful indicator of eutrophication. In Kaneohe Bay, though, very little change in community structure accompanied the sewage diversion. In fact, relative abundances of both macroplankton and microplankton remained the same, with a few exceptions. Barnacle larvae decreased dramatically, probably because of diminished adult fecundity. Among the holoplankton, the cladoceran *Evadne* spp. and the harpacticoid copepod *Euterpina acutifrons* showed a decrease in relative abundance. The relative abundances of the remainder of the common zooplankton taxa changed little with sewage diversion. Comparison with the historical data (e.g., Bartholomew 1973; Peterson 1975) also showed few consistent differences.

GENERAL BENTHOS TRANSECT DESCRIPTIONS: It is useful to consider the taxonomic composition of the benthos in detail. In contrast to the zooplankton, the benthic biota exhibited a strong horizontal and temporal gradient of sewage influence.

Aspects of the benthic community were sampled at four localities in the bay (Figure 36). The southern basin was represented by a single station (OF/SE), the CE sector by one station, and NW by two stations (NW fringe and patch). Three major transects were established on the fringing reef of each sector, extending from the lagoon floor, up the slope, and across the reef flat to within 20–30 m of the shoreline. A fourth transect, in the NW sector, extended from the lagoon floor onto a patch reef that is relatively free of obvious direct land-derived influence.

The OF/SE transect was on the fringing reef approximately 800 m downcurrent of the prevailing flow from the Kaneohe sewer outfall and was also immediately downcurrent of a stream mouth. The transect thus received freshwater and silt influence during periods of high runoff and was subject to chronic influence of the sewage discharge during the prediversion period. The transect extended from a maximum water depth of 7.5 m immediately lagoonward of the base of the reef slope to within 20 m of the shoreline. The transect length was approximately 120 m. General biological characteristics that distinguish this transect were paucity of live coral, paucity of large fleshy algae, and abundance of suspension- and filter-feeding organisms (especially sponges, tunicates, and barnacles). Soft corals (zoanthid coelenterates rather than scleractinian corals) dominated the landward end of the transect. The lagoon floor at the base of the transect was covered by fine mud, with local hard-bottom areas where the reef had been dredged. The reef slope and flat had mud, sand, and rubble; the rubble largely consisted of oyster and barnacle shell debris as well as disintegrating reef limestone. The mud had a conspicuous component of red, land-derived material. There were no extensive hard-bottom areas on this transect; apparent hard bottom or large pieces of rubble on the slope and reef margin crumbled easily. The water along the transect was noticeably turbid. Prediversion chlorophyll-*a* values there averaged about 10 $mg \cdot m^{-3}$, over twice the average of the OF water-sampling station (Table 11).

The CE transect was across a fringing reef removed from the direct influences of either sewage or most stream runoff, although Banner (1968) demonstrated that lowered salinity from extreme runoff can affect reefs along the entire shoreline of the bay. The transect extended from a water depth of 13.5 m on the lagoon floor to within 30 m of the shoreline. The transect length was ap-

proximately 250 m. The lagoon floor had a mud bottom; the reef slope had considerable coral rubble, and the large green alga *Dictyosphaeria cavernosa* was a conspicuous component of the slope. The upper slope and reef crest had encrusting coralline algae, relatively diverse and abundant corals, and a large amount of *D. cavernosa*. Corals occurred in low spots on the reef flat but became progressively less abundant from the reef crest toward the shoreline. Fleshy algae increased in abundance toward the shoreline, and were established on the widespread hard-bottom areas. Calcareous sand covered much of the flat.

The NW sector fringing reef transect was influenced by a nearby stream. Fine lagoonal sediments draped relatively high up on the reef slope, making the lagoon floor at the base of that transect only about 4.5 m deep—significantly shallower than in most areas of the lagoon. The transect extended from that depth, up the slope and across the reef flat for a total length of about 260 m. The slope had relatively high coral cover, interspersed with mud. There were a few corals on the rather poorly developed reef crest, and the reef flat was relatively muddy but with conspicuous fleshy algae. The water across this transect was often turbid with fine sediment, and the sediment on the transect was largely red terrigenous mud.

Samples were also collected on a patch reef transect in the NW sector, approximately 650 m seaward of the NW fringing reef transect. This relatively short distance was sufficient to remove the patch reef from major obvious land influences such as the high sediment loading that occurred on the fringing reef. Benthic sampling on this transect was undertaken on the lagoon floor (11 m) and up the slope onto the reef flat. In general, the slope and crest had better developed coral growth than the nearby fringing reef transect. Sediments on this transect were virtually free of obviously land-derived material.

Sampling for total biomass was undertaken at two-month intervals. Sampling for gross taxonomic analysis was undertaken every six months. Details of methods are presented in the Appendix.

TABLE 28

NUMBER OF BENTHIC ALGAL TAXA PRESENT BEFORE AND AFTER SEWAGE DIVERSION

	NW	CE	SE/OF
Prediversion	22	21	19
Postdiversion	21	16	16
Entire period	23	21	21
Found only at this station (entire period)	4	4	5

NOTE: Based on 186 algal samples.

BENTHIC ALGAE: A large number of algal taxa are present in the bay. Soegiarto (1973) reported 87 species; however, most of that taxonomic diversity occurs in the outer portion of the bay. We found 34 species at our sampling stations within the inner bay (Table 28). The data suggest very little taxonomic differentiation among sectors and no significant compositional response to diversion (Kruskal-Wallis test; $n = 137$). Most algae in the bay were found on shallow reef flats where light levels were high. The sole significant exception to this generality was *Dictyosphaeria cavernosa*, a bulbous green alga that was abundant on the reef slopes of the CE sector.

Despite the general homogeneity of algal composition throughout the bay, obvious differences can be seen among the sectors. In particular, *Ulva* tended to dominate the biomass of the OF/SE sector and became less abundant after sewage diversion. This conspicuous alga was not recorded at the other sampling stations. *Dictyosphaeria* was absent from the OF/SE transect, dominant on both the slope and the reef flat at CE, and present at NW.

Significant aspects of algal variation were well represented by total dry weight standing crop (Figure 37, Table 29). The algal standing crop showed strong spatial patterns within the bay. In general, coverage was low on the reef flat of the SE sector and highest in the CE sector, regardless of season. There was also substantial temporal (at least partly

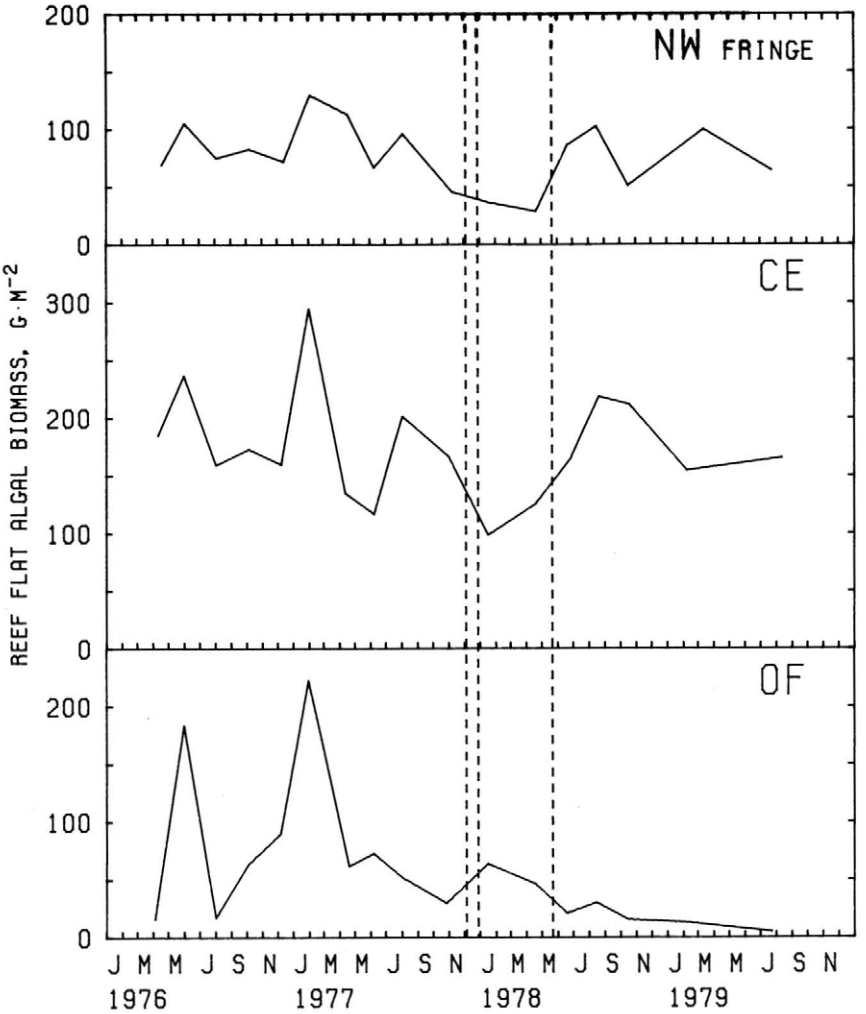


FIGURE 37. Hard-bottom algal biomass. Vertical dashed lines as in Figure 10.

TABLE 29

CHANGE IN MACROTHALLOID ALGAL BIOMASS FROM BEFORE TO AFTER SEWAGE DIVERSION

	MEDIAN BIOMASS						
	PREDIVERSION		POSTDIVERSION		KRUSKAL-WALLIS	DEGREES OF	
	g·m²	*N*	g·m²	*N*	H	FREEDOM	SIGNIFICANCE
NW	73	30	51	21	3.31	1	N.S.*
CE	169	20	150	14	0.44	1	N.S.
OF/SE	51	25	16	27	4.25	1	$P < 0.05$

*Not significant.

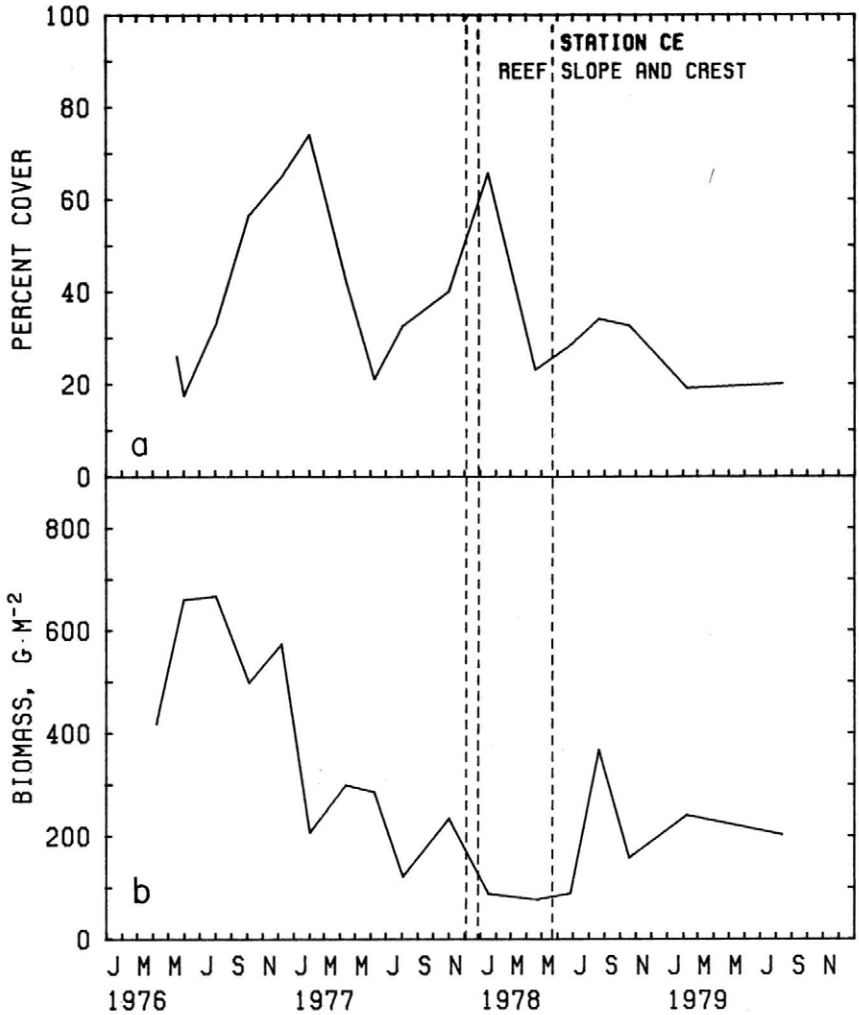


FIGURE 38. Biomass and percent cover by *Dictyosphaeria cavernosa* on the reef slope and crest in the CE sectors. Vertical dashed lines as in Figure 10.

seasonal) variation. The standing crop of algae on the reef flats differed significantly among sectors before diversion (Kruskal-Wallis $H = 25.55$; $p < 0.0001$) and remained different among sectors after diversion ($H = 36.13$; $p < 0.0001$). The standing crop did not change significantly on the NW and CE reef flats but declined by about 60 percent ($p < 0.05$) on the SE sector flat (Table 29). Note that the decrease in the SE sector biomass actually preceded the diversion (Figure 37). The apparent explanation is that the diversion occurred when biomass was low from normal seasonal oscillations; biomass rose slightly but never recovered to the prediversion level.

Only the CE sector station had a significant algal biomass (dominated by the single taxon, *Dictyosphaeria cavernosa*) on the reef slope and crest. This population declined markedly (Figure 38, Table 30). As noted for the SE sector reef flat biomass, *Dictyosphaeria* biomass on the reef slope of the CE sector was low from normal temporal oscillation when sewage was diverted.

The percent cover by *Dictyosphaeria* at the

TABLE 30

CHANGE IN DRY WEIGHT OF *Dictyosphaeria cavernosa* ON THE REEF SLOPE AND CREST OF THE CE SECTOR ($g \cdot m^{-2}$)

	PREDIVERSION			POSTDIVERSION		
	Mean ± 95%	*N*	Median	Mean ± 95%	*N*	Median
Slope	386 ± 123	20	239	156 ± 29	14	151
Crest	423 ± 89	20	403	192 ± 98	14	122

TABLE 31

INVENTORY OF BENTHIC ALGAL STANDING CROP BEFORE AND AFTER SEWAGE DIVERSION (dry weight, in tons)

PHYSIOGRAPHIC ZONE	NW	CE	OF/SE	TOTAL
Slope + crest (available area, $10^6 m^2$)	0.32	1.07	0.86	2.25
pre	0	418	0	418
post	0	172	0	172
Flat (available area, $10^6 m^2$)	1.51	1.36	0.70	3.57
pre	140	249	48	437
post	111	220	18	349
Total (available area, $10^6 m^2$)	1.83	2.43	1.56	5.82
pre	140	667	48	855
post	111	392	18	521

NOTE: Prorated from dry weight means, as discussed in text, assuming algae cover available substratum (solid + rubble + algae, Table 16).

CE station showed a much clearer seasonal oscillation than did biomass (compare Figure 38 top and bottom), with high cover in the fall and winter. Although biomass better reflects the alga as a time-varying nutrient sink, the graph of percent cover better emphasizes the failure of *Dictyosphaeria* to recover its prediversion abundance after sewage diversion.

Data from the sampling stations can be used to estimate the approximate bay-wide decline in algal biomass. Recent analyses of algae from Kaneohe Bay (Atkinson and Smith, submitted) indicated that the dry weight of these algae averages about 27 percent carbon and that the C : N : P atomic ratio is approximately 640 : 30 : 1. In other words, they have about one-fifth the nutrient content of plankton (Redfield, Ketchum, and Richards 1963).

Table 31 summarizes the dry-weight data. From the above figures, it can be estimated that algal carbon dropped from 230 to 140 tons after sewage diversion; algal nitrogen from 900 to 550 kmoles; and algal phosphorus from 30 to 18 kmoles. Most of the biomass and most of the decline were in the CE sector and involved the changing *Dictyosphaeria* biomass on the reef slopes.

BENTHIC ANIMALS AND FISHES: Kaneohe Bay harbors a complex assemblage of benthic animals and associated reef fishes. In particular, the hard substrata provide abundant and diverse microhabitats and support a high biomass and diversity of cryptofauna. Most benthic taxa that have been found in Hawaiian waters have been reported from Kaneohe Bay (see, e.g., Gordon and Helfrich 1970), and most benthic organisms common in one part of the bay are found in some numbers throughout it. As far as we could ascertain, neither the sewage discharge into the bay nor its diversion from the bay

TABLE 32

NUMBERS OF COMMON TAXA OF CONSPICUOUS INVERTEBRATES IN SEVERAL MAJOR GROUPS, FOR LAGOON, REEF SLOPE, AND REEF FLAT

	NW			CE			SE/OF		
TAXONOMIC GROUP	L	S	F	L	S	F	L	S	F
Porifera (sponges)	0	5	1	0	3	1	0	12	3
Cnidaria less stony corals	0	2	2	0	3	3	0	3	5
Stony corals	0	7	0	0	7	3	0	3	0
Annelida	0	0	0	0	0	0	0	0	3
Mollusca									
Gastropoda	0	0	2	0	8	8	0	5	6
Bivalvaia	0	0	2	0	1	3	0	1	5
Crustacea									
Cirripedia (barnacles)	0	0	0	0	0	0	0	4	0
Decapoda	4	2	4	4	2	3	4	0	1
Stomatopoda	0	0	0	0	0	0	0	0	1
Echinodermata	0	2	1	0	3	3	0	1	0
Ascidiacea (tunicates)	0	1	0	0	2	0	0	11	1

NOTE: L = Lagoon; S = Reef slope; F = Reef flat.

resulted in the total elimination of any taxon from any part of the bay.

Because of the high diversity and biomass of the bay benthos and the heterogeneity of substratum type and organism distribution, it was not practical to obtain statistically valid comprehensive taxonomic detail on a large number of samples. For quantitative analyses we therefore devoted our attention to benthic biomass, and gave relatively little attention to taxonomic detail.

A qualitative look at conspicuous macrofaunal benthic taxa merits attention. These taxa exclude cryptofauna, which were dominated by smaller polychaetes and crustaceans and which accounted for most of the biomass of many soft- and hard-bottom samples (see, e.g., Brock and Brock 1977; White 1980). Several patterns emerged from presence-absence data gathered on our transects (Table 32).

The reef slopes had the greatest diversity of conspicuous benthic taxa, with the SE/OF slopes being the richest. The flats were next in diversity, with about the same number of taxa at SE/OF and CE. The lagoon had a very low diversity of conspicuous organisms and the same taxa throughout the bay. The SE/OF sector differed most obviously from the other sectors by the diversity of filter feeders such as conspicuous sponges, polychaetes, tunicates and by the paucity of echinoderms. Subphyletic differences can also be seen. Barnacles, some mollusks, and two species of zoanthids were common at SE/OF but rare elsewhere. Although corals were found in the SE/OF sector, they were neither as diverse nor as common (see also Table 16) as elsewhere. The predominant organisms at the SE/OF station were primarily filter feeders or deposit feeders relying on detritus in the water column or in the sediments. Strictly on the basis of number of taxa, the SE/OF sector appeared to have been enriched rather than depleted by the stresses imposed. There has been, however, a shift away from corals, the most conspicuous biological component of coral reefs.

Most of the taxa listed in Table 32 are organisms primarily associated with hard bottom. Compositional variation of the soft bottom, especially the lagoon floor, was slight (Brock and Smith, submitted). In temperate bodies of water, soft-bottom communities show large compositional responses to changing sewage loading (Otte and Levings 1975; Poore and Kudenov 1978*a*, 1978*b*). We suspect that the difference between the lack of response of Kaneohe Bay lagoon-floor communities to sewage and the more striking responses at other localities that have been studied largely reflects a difference in the level of stress. The sewage loading in Kaneohe Bay was small in comparison with some other examples studied, and there was no stress imposed by high biological oxygen demand and low oxygen levels.

Reef fishes on the slopes and crests showed prominent differences among the sectors (Table 33). Of particular interest, the checklist of common taxa is similar for the NW and CE sectors, with over 40 species. Only 6 species of reef fishes were commonly found on the slopes and crests of the OF/SE sector. This attenuation apparently largely reflects

TABLE 33

NUMBERS OF FISH SPECIES COMMONLY ENCOUNTERED IN KANEOHE BAY BEFORE SEWAGE DIVERSION

	NW	CE	SE/OF
Resident on reef slopes and crests	40	43	6
Wandering species	3	6	0
Encountered in water column above lagoon floor	15	15	15

the paucity of satisfactory shelter because of the absence of corals. As with benthic organisms, fishes of the lagoon floor showed no variation among sectors.

The trophic structure of the fishes in the CE sector was dominated by planktivorous species (Brock, Lewis, and Wass 1979). This contrasts with other reefs, which generally are dominated by predators on larger prey (Al-Hussaini 1947; Goldman and Talbot 1975; Hiatt and Strasburg 1960; Randall 1963, 1967; Talbot 1965; Talbot and Goldman 1972). This dominance of planktivores apparently reflected the high plankton biomass in the water column. In view of the small change in plankton biomass, especially outside the southern basin, we do not expect a shift in trophic structure of the fish community, and none occurred during our study.

In no case can we demonstrate that the diversion of sewage caused the appearance or disappearance of benthic taxa in any sector of the bay. Early information (MacKaye 1916) suggests that the generally poor reefs of the SE/OF sector have been that way for at least 60 years. Data gathered approximately 40 years before our investigation from both natural fouling communities and communities developed on fouling panels (Edmondson and Ingram 1939; Ingram 1937) further support this interpretation. Probably siltation and freshwater from runoff have affected the reefs as much as sewage. Dredging in the 1930s and 1940s (Hollett 1977; Roy 1970) obviously decimated communities on specific reefs. Many of the dredged areas have subsequently been recolonized.

In 1965, runoff killed reef organisms of fringing reefs throughout much of the bay (Banner 1968, 1974). Recovery of biota on the reef flats, crests, and upper reef slopes proceeded in directions apparently influenced by the increasing sewage load. The OF/SE sector developed toward a filter-feeding community, in apparent response to high particulate organic carbon. The CE sector recovered toward a community with high algal (*Dictyosphaeria cavernosa*) biomass. This response has been interpreted to have been caused by the sewage (e.g., Banner 1974), although the pattern of recovery may be more complex than a simple response to elevated nutrients. The NW sector reef flat showed no apparent response to the sewage as it recovered from the freshwater kill.

The changes that occurred in the benthic animals in response to sewage diversion are shown strongly in the animal biomass data. Table 34 presents the mean dry-weight biomass of organisms in sediments and hard substrata before and after sewage diversion. The infaunal standing crop in the soft sediments was consistently low and showed relatively little response to sewage diversion. Brock and Smith (submitted) consider that in such soft-sediment environments the substratum (i.e., habitat) is a more immediately limiting resource than is food.

By contrast, the hard substratum showed high biomass at the OF/SE transect, large variation among the transects, and evidence of responses to sewage diversion. Differences among transects within physiographic zones were highly significant before and after diversion (Kruskal-Wallis tests, $p < 0.01$). Inspection of Table 34 makes it obvious that most of the difference among transects was contained in the very high biomass of the OF/SE transect. Before sewage diversion, cryptofaunal biomass in the hard substrata of the CE and NW transects was around 50 $g \cdot m^{-2}$, whereas the biomass was about 300 $g \cdot m^{-2}$ at SE/OF.

With sewage abatement, the animal biomass of the hard-substratum cryptofauna decreased significantly in all physiographic zones at all of the fringing reef transects ($p < 0.03$, Kruskal-Wallis tests), but only on the reef crest of the NW sector patch reef ($p < 0.002$). The decrease at the NW and CE

TABLE 34

BENTHIC INFAUNAL-CRYPTOFAUNAL ORGANISM BIOMASS ON THE FOUR TRANSECTS BEFORE AND AFTER SEWAGE DIVERSION
($g \cdot m^{-2}$ dry weight)

PHYSIO-GRAPHIC ZONE	SE/OF			CE			NW FRINGE			NW PATCH		
	MEAN ± 95%	*N*	MEDIAN	MEAN ± 95%	*N*	MEDIAN	MEAN ± 95%	*N*	MEDIAN	MEAN ± 95%	*N*	MEDIAN
Lagoon floor (soft)												
pre	6 ± 5	8	3	3 ± 3	11	1.5	0.4 ± 0.2	8	0.2	6 ± 5	8	3
post	1 ± 0.8	8	0.6	0.6 ± 0.2	7	0.5	7 ± 7	6	8	3 ± 1.5	9	2
Reef slope (hard)												
pre	220 ± 75	12	212	44 ± 15	12	40	52 ± 22	10	41	21 ± 9	8	17
post	39 ± 24	10	40	11 ± 7	10	7	18 ± 14	8	9	17 ± 16	4	10
Reef crest (hard)												
pre	412 ± 277	12	210	28 ± 17	12	21	78 ± 15	12	73	37 ± 11	10	33
post	31 ± 10	10	26	11 ± 5	10	8	19 ± 6	10	18	14 ± 8	10	10
Reef flat (hard)												
pre	337 ± 117	12	265	69 ± 28	14	47	75 ± 21	10	67			
post	133 ± 66	10	132	31 ± 20	10	19	48 ± 27	10	33			
Reef flat (soft)												
pre	17 ± 5	10	12	27 ± 20	16	10	no data*					
post	11 ± 6	10	6	8 ± 5	9	6	6 ± 4	6	5			

*Indicates samples with high terrigenous fractions.

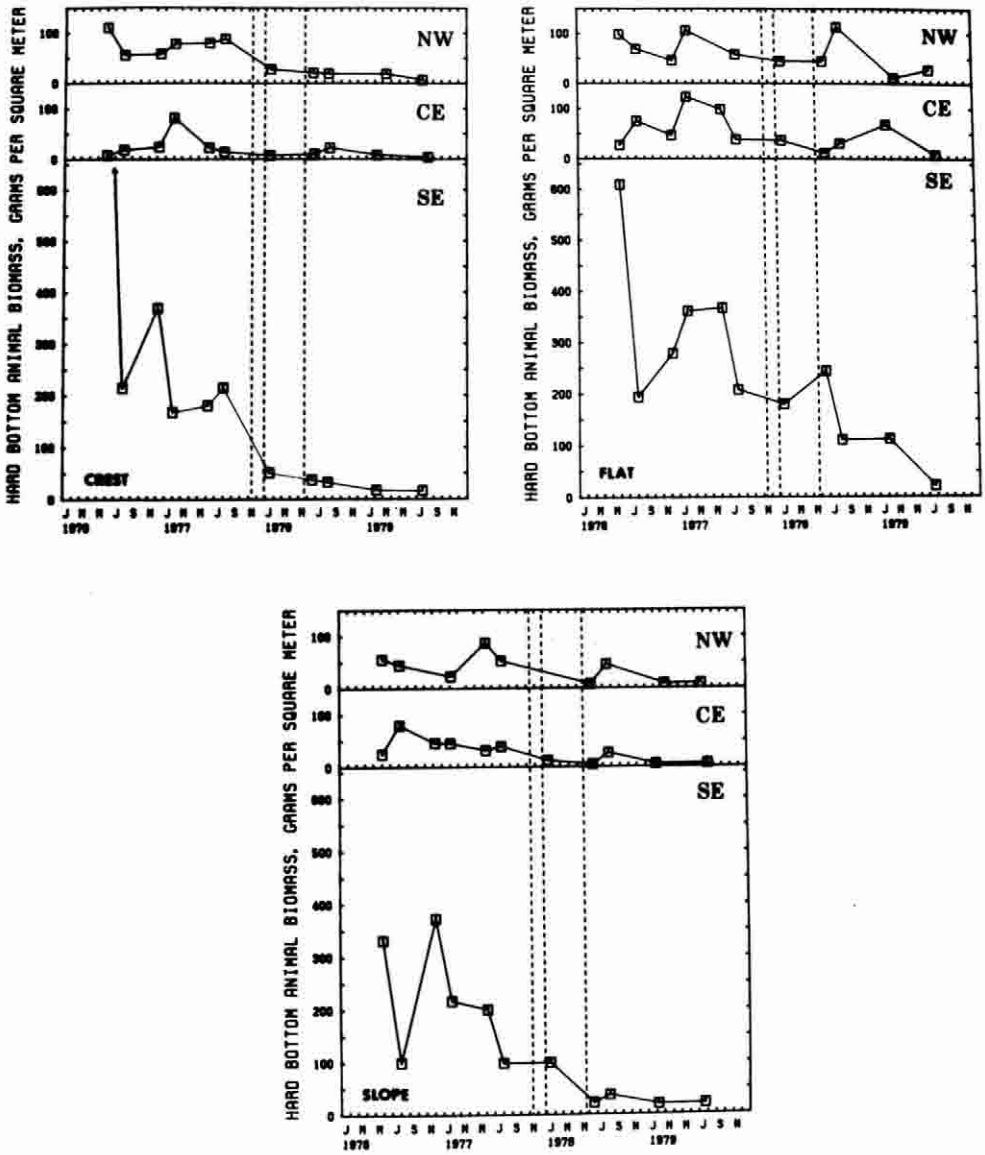


FIGURE 39. Hard-bottom benthic animal biomass in Kaneohe Bay. Vertical dashed lines as in Figure 10.

transects was from approximately 50 to approximately 20 $g \cdot m^{-2}$, while the decrease at the OF/SE transect was from approximately 300 to approximately 70 $g \cdot m^{-2}$. It is apparent from plots of cryptofaunal biomass through time (Figure 39) that most of this drop in the biomass occurred well within the first year of sewage diversion. The postdiversion period was insufficient to determine whether the OF/SE biomass would eventually stabilize near that of the other transects.

Cryptofauna of the reef crest apparently provided the largest and most consistent response to sewage diversion. This may have been related to the high standing crop and relative homogeneity of this habitat. High but variable standing crop values for crypto-

fauna on the reef flat were the result of abundant colonial zoanthids on the OF/SE transect and random encounters with large motile invertebrates (e.g., crabs, gastropods) on the CE transect.

The benthic animal biomass in various substrata prorated over the entire bay presents a clear picture of total animal biomass change with sewage diversion (Table 35). Before diversion, over half the benthic animal standing crop was confined to the southern basin (only a quarter of the bay area, Table 2). The benthic animal dry-weight biomass before sewage diversion was almost 1000 tons. After diversion, animal biomass decreased to near 400 tons and the biomass became more evenly distributed throughout the bay.

From Vinogradov (1953) we estimate that the benthic animal dry weight was about 30 percent organic carbon and that the C : N : P atomic ratio was about 130 : 40 : 1. Thus, the carbon storage in animal biomass dropped from approximately 300 to 100 tons; nitrogen dropped from about 8000 to 3000 kmoles; and phosphorus dropped from about 190 to 60 kmoles.

TABLE 35

BENTHIC ANIMAL STANDING CROP ESTIMATES BASED ON DATA FROM TABLES 11 AND 34 PRORATED OVER THE ENTIRE BAY
(Metric tons, dry weight)

PHYSIOGRAPHIC ZONE	NW	CE	SE/OF	BAY TOTAL
Lagoon floor (soft)				
pre	11.1	21.6	25.5	58.2
post	17.4	4.3	4.3	26.0
Reef slope (hard)				
pre	18.1	41.8	202.4	262.3
post	8.8	10.5	35.9	55.2
Reef slope (soft)				
pre	4.3	2.1	10.4	16.8
post	6.7	0.4	1.7	8.8
Reef crest (hard)				
pre	8.1	4.8	16.5	29.4
post	2.4	1.9	1.2	5.5
Reef crest (soft)				
pre	2.8		0.7	3.5
post	0.8		0.4	1.3
Reef flat (hard)				
pre	113.3	100.7	235.9	449.9
post	72.5	45.3	93.1	210.8
Reef flat (soft)				
pre	74.4	47.8	13.4	135.6
post	22.3	14.2	8.7	45.2
Totals				
pre	232.1	218.8	504.8	955.7
post	130.9	76.6	145.3	352.8

NOTE: Animal Biomass in soft substratum occurring in the reef slope habitat is calculated using adjacent lagoon floor estimates and in the reef crest biotope using soft substratum reef flat estimates. Northwest sector estimates are made using biomass means from the NW Fringe and NW Patch reef sampling sites.

Summary

In this section we have discussed data on ecosystem composition. Various particulate and dissolved inorganic substances showed gradients from high concentrations in the southern basin to low in the north. They also decreased following sewage diversion, apparently to nearly presewage levels. Dissolved inorganic and particulate nitrogen decreased following sewage diversion by about 30 percent in the southern basin. Chlorophyll and microplankton and macroplankton biomass also decreased by about 30 percent. Estimated detrital carbon and extinction coefficient, however, decreased by only about 10 percent. The influence of wind on water clarity partially masked a significant response to sewage diversion.

The benthic biota showed a strong gradient from typical reef communities in the north to a filter-feeding community in the south, with an attendant increase in biomass. The decline in benthic biomass was proportionately greater than that seen in the water column, but the benthic biomass and taxonomic composition had not returned to presewage conditions by the end of the study. This may reflect an insufficient post-diversion monitoring period, irreversible shifts in community structure, or shifts arising from factors other than sewage.

An important conclusion of this section is that the observable response of the entire system to sewage diversion was very rapid. We observed no continuing downward trend in the water column after the diversion period, and those variables for which historical data are available appear to have decreased to their presewage values.

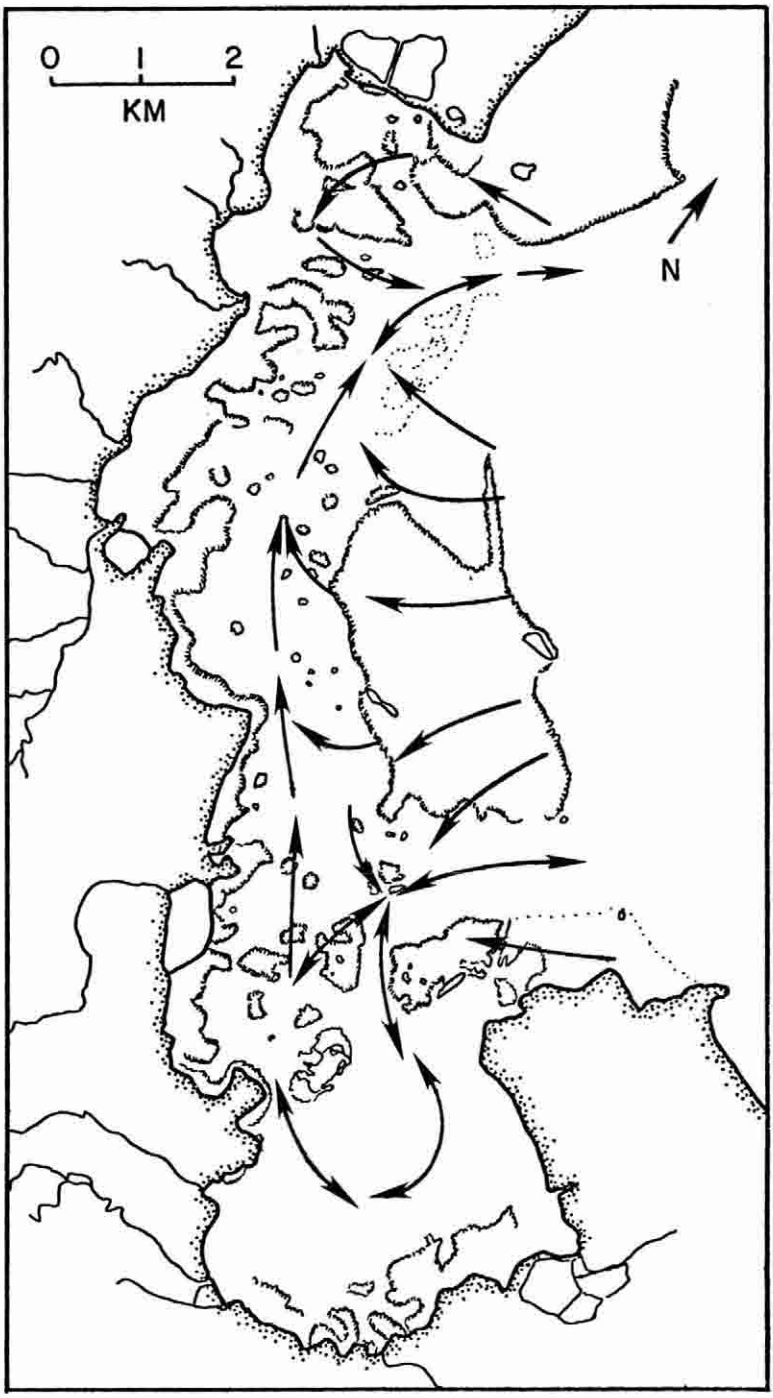


FIGURE 40. Generalized circulation pattern in Kaneohe Bay. Modified from Bathen (1968).

ECOSYSTEM DYNAMICS

In previous sections we have introduced the environmental setting for the Kaneohe Bay experiment and described the composition of the bay and the change of composition after sewage diversion. In this section we consider how the bay processes materials, in particular, the exchange of water between the bay and the ocean; the fluxes of materials with that exchanging water; the fluxes due to internal, biologically mediated processes; water clarity in relation to the processes of material fluxes; and the effects of sewage and its diversion on the biological processes of Kaneohe Bay. In much of the section we concentrate on variation in the southern basin, that portion of the bay most directly affected by sewage diversion.

Bay Flushing

The primary significance of water circulation in relation to the present analysis is the dispersal of materials, including the exchange of materials between the bay and the ocean. We have used information available in the literature together with our own observations to arrive at a generalized description of circulation. We then use mass-balance calculations to present a simple numerical model of bay water volume transport and exchange with the ocean. References on bay circulation include Bathen (1968); Dames and Moore (1977); Niemeyer (1978); Runchal (1978); and Sunn et al. (1976).

Circulation of water in the bay is governed by tidal flow, wind-driven mixing and advection, wave action outside the bay, and inflow of stream water. Under most conditions, ocean water enters the bay across the Outer Bay barrier reef, which forms a sill between the ocean and the transition zone of the Inner Bay (Figure 40). The strength of this flow depends on the changing tidal stage and on the height of waves breaking on that reef. The channels at either end of the barrier reef have a flow that reverses in response to the combined force of waves breaking on the outer-bay reefs and tidal state. The flow of deep water within the Inner Bay is relatively sluggish. Wind stress mixes water vertically, and a combination of wind and tides accounts for horizontal advective flow.

With available data, it is difficult to arrive at a satisfactory basis for treating the NW and CE sectors of the bay as distinguishable circulation cells; it is therefore more useful to consider the transition zone (NW + CE sectors) as a single circulation unit. The transition zone exhibits good water exchange with the ocean, because both the shallow, largely inward flow across the barrier reef and the reversing flow through the channels communicate almost exclusively between the ocean and this portion of the bay. The southern basin (SE + OF) is largely isolated from direct oceanic exchange, perhaps receiving a small amount of oceanic water through the channel northeast of Coconut Island (Figure 40).

Each of these two regions is relatively well mixed vertically and horizontally, with little evidence of significant compositional gradients under most conditions. There are two significant exceptions to this generality: With low wind, a vertical gradient in water clarity can develop (Figure 32); and salinity-mediated density stratification can also develop when freshwater input is high (Figure 19). Directly relevant to this section and important to dispersal of material within the bay is the existence of a wedge of low-density water that develops locally along the shoreline. One area with such a front along the shore entrained the sewage delivered to the OF sector and was the object of interest and study during our investigation (Kimmerer, Walsh, and Hirota 1981). This feature is described briefly below.

When winds blow onshore (0°–135°) for several hours, a front develops near the municipal sewer outfall as wind stress opposes the spread of freshwater entering the OF sector of the bay. With sufficient particulate materials entrained in the water, the front is visible as a distinct plume (Figure 41). The front can also be detected by a sharp horizontal change in density indicated by differences in salinity and temperature; water landward of the front is ordinarily 0.5–1.0‰ less saline and 0.2° C warmer than on

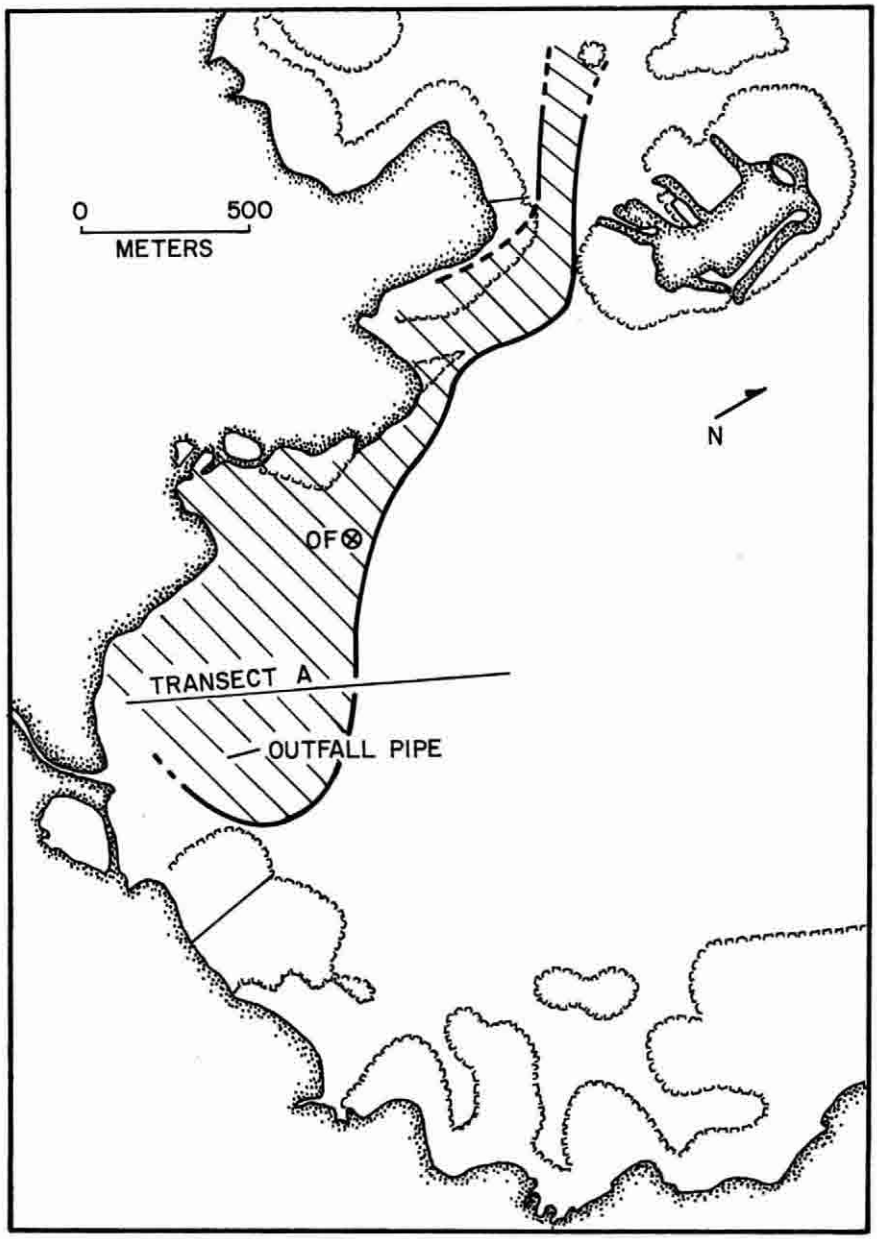


FIGURE 41. Southern basin of Kaneohe Bay showing location of the outfall pipe, outfall sampling station (OF), and the low-density plume on 17 May 1977.

the seaward side. In the absence of wind, freshwater entering the OF sector spreads laterally and results in vertical stratification but little horizontal density gradient and no strong pattern of water clarity.

Nutrients and particulate matter discharged behind the front by streams or sewage remained trapped there, producing a readily visible plume of water discolored by blooms of phytoplankton, especially large

TABLE 36

NET VOLUME FLUX AND NET NITROGEN FLUX FROM THE OF REGION, THROUGH THE CHANNEL WEST OF COCONUT ISLAND, TO THE CE SECTOR AS A FUNCTION OF WIND DIRECTION

DATE	WIND DIRECTION (°)	WIND SPEED ($m \cdot sec^{-1}$)	VOLUME FLUX ($m^3 \cdot day^{-1}$)	NET NITROGEN FLUX ($kmoles \cdot day^{-1}$)
Prediversion				
9 Aug 1977	022–050	4	0	0
23 Aug 1977	045–070	7	3.1×10^6	20
30 Aug 1977	045–070	6	2.6×10^6	26
26 Sep 1977	022–070	3.5	2.4×10^6	16
Postdiversion				
16 Mar 1979	045	6.0	3.9×10^6	2.4

SOURCE: Kimmerer, Walsh, and Hirota (1981).

diatoms. In addition to low density, the plume was characterized by high levels of all nutrients, various measures of particulate matter, and dissolved organic matter. The transient nature of this plume at least partly explains the highly variable nutrient and chlorophyll composition observed at the OF sampling station (Figures 20 to 25).

With a wind direction of 0°–45°, the plume remains in the southern basin, losing material by diffusion across the front and by sedimentation. When winds blow from 45°–135°, the plume flows through the channel west of Coconut Island and into the CE sector, where it disperses. In the channel, the plume occupies only the upper 1–3 m of the water column, and is virtually indistinguishable in density from other surface water in the channel. However, it remains visible, and is carried through the channel by a wind-driven surface drift of up to 15 $cm \cdot sec^{-1}$. On five occasions, four before and one after sewage diversion, we sampled and measured currents in the channel to determine volume and mass flux out of the channel. Table 36 shows that when winds were blowing from 45°–135°, the volume flow was about $3 \times 10^6 m^3 \cdot day^{-1}$. Nitrogen fluxes before sewage diversion ranged from 16 to 26 $kmoles \cdot day^{-1}$, close to the input rate of nitrogen into the OF sector (26 $kmoles \cdot day^{-1}$, Table 7). Following diversion, the frontal volume flux into the CE sector remained the same as it was before diversion (Table 36), but nitrogen mass flux decreased to about 2 $kmoles \cdot day^{-1}$—about equal to the nutrient input by the streams on the measurement date. The balance of frontal flow was not changed significantly by termination of sewage discharge, although the nutrient transport and plume visibility did change.

The wind direction required for plume flow occurs about half of the time (Figure 12), suggesting that about half of the nitrogen discharged from the Kaneohe sewage treatment plant was directly advected out of the southern basin into the CE sector. It follows that the mean flux of nitrogen from the OF sector into the SE sector was approximately half of that delivered by sewage discharge.

Except for this intermittent and localized phenomenon of nearshore frontal flow, the two major geographical units of the bay (the southern basin and the transition zone, Table 2) can be treated as well-mixed circulation cells in a simple two-compartment flushing model (Figure 42). It is assumed that no term besides tide is quantitatively significant to the net flow of water between compartments and that water within each sector is well mixed.

Tides in Kaneohe Bay are mixed semidiurnal, and the mean tidal amplitude is 377 mm (U.S. Department of Commerce). Using the areas given in Table 2, one can calculate the volume of water that must enter and leave a

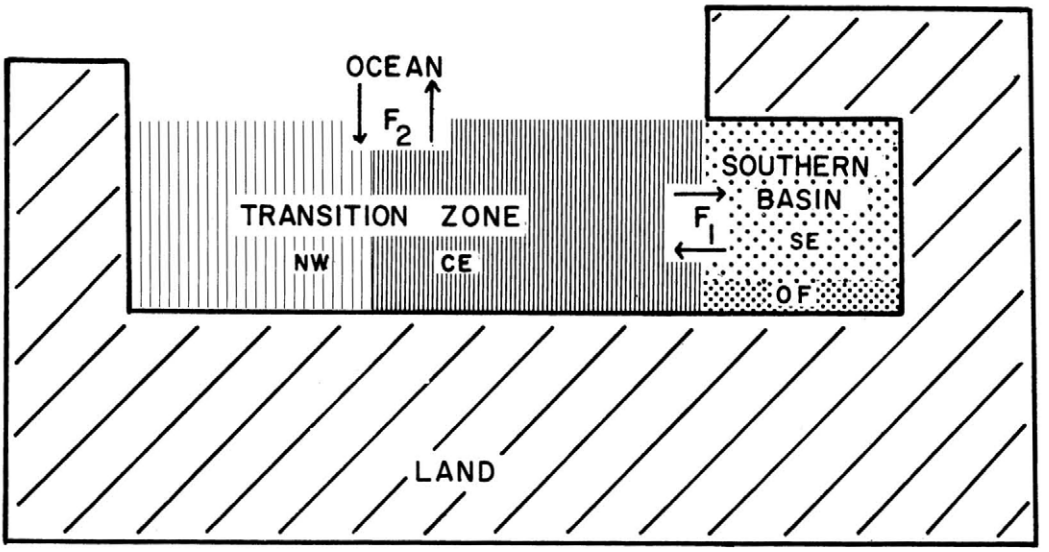


FIGURE 42. Two-compartment tidal model of bay flushing. F_1 and F_2 are volume flows.

compartment to yield this amplitude. For the entire bay:

$$F_{Bay} = (0.377\ \text{m}) \cdot (31.47 \times 10^6 \text{m}^2) = 11.86 \times 10^6 \text{m}^3$$

per tidal cycle. Because this water flows into the transition zone or through it to exchange with the southern basin, this volume flux also represents the transition zone. For the southern basin:

$$F_{Southern} = (0.377\ \text{m}) \cdot (8.37 \times 10^6 \text{m}^2) = 3.16 \times 10^6 \text{m}^3$$

per tidal cycle. Taking the average tidal cycle to be 12 h 25 m (0.517 days·tide^{-1}), the daily exchange volumes are calculated to be:

$$F_{Southern} = 6 \times 10^6 \text{m}^3 \cdot \text{day}^{-1};$$

$$F_{Bay} = 23 \times 10^6 \text{m}^3 \cdot \text{day}^{-1}.$$

The flushing time (T) of the various bay compartments, based on the assumption of complete mixing during each total excursion, can be obtained by dividing that compartment volume by the appropriate volume fluxes. Thus:

$$T_{Bay} = (265.68 \times 10^6 \text{m}^3)/(23 \times 10^6 \text{m}^3 \cdot \text{day}^{-1}) \cong 8 \text{ days};$$

$$T_{Southern} = (79.59 \times 10^6 \text{m}^3)/(6 \times 10^6 \text{m}^3 \cdot \text{day}^{-1}) \cong 13 \text{ days}.$$

Unless there is some major flow not recognized by this simple tidal model (e.g., substantial wind- and wave-driven surface inflow and deep outflow to compensate this nontidal input), these estimates adequately summarize the flushing characteristics of the bay. Incomplete mixing and the frontal flow along the shoreline seem unlikely to alter the volume transport calculations by more than about $\pm 1 \times 10^6 \text{m}^3 \cdot \text{day}^{-1}$.

It would be desirable to confirm the model presented with independent estimates of bay flushing. We considered a salt and freshwater budget and a heat budget as possible independent checks of bay flushing. Both calculations are defeated by extremes:

Bay flushing was large ($\approx 23 \times 10^6 \text{m}^3 \cdot \text{day}^{-1}$) compared with average freshwater input ($\approx 0.3 \times 10^6 \text{m}^3 \cdot \text{day}^{-1}$) over the course of our investigation (Table 4). The observed salinity reduction ($\approx 0.2‰$; Figure 18) and the expected reduction ($\approx 0.3‰$) are close to one another, but are both too small to be used in any quantitatively satisfactory manner.

Bathen (1968) presented a heat budget which balanced over an annual cycle to within approximately 10 cal·cm^{-2}·day^{-1}. In fact, the bay is 0.5° warmer than the

ocean over the course of a year (see Water Composition). The tidal flux data suggest that there should be a net advection of about 40 cal · $cm^{-2} \cdot day^{-1}$; an uncertainty of at least 5 percent in calculating heat loss from evaporation and back radiation precludes quantification of advective heat flux.

We conclude from these preliminary analyses that the bay salinity and temperature are insufficiently sensitive to be used as independent quantitative measures of flushing. However, neither of these variables gives reason to believe the tidal model is grossly in error. That model is therefore used in the next section as a semiquantitative estimator of the flux of biologically active materials.

Nutrient Cycling in the Southern Basin

If materials introduced into the water column of a circulation cell within the bay are not consumed or produced within that cell, they may be treated as conservative tracers to estimate water flushing independently of direct measures of volume flux. In discussing bay flushing, we considered such calculations for salt and heat, but concluded that uncertainties in material balances precluded the use of such calculations as independent checks on the tidal flux model of bay flushing.

An alternative use of material balances is to consider materials that are consumed or liberated internally and to derive some understanding of the net internal, nonconservative alterations of those materials (i.e., production or consumption within the cell). We will here explore such calculations for the southern basin of Kaneohe Bay in order to understand aspects of nitrogen and phosphorus flux within that portion of the bay. Consider the following simple mass flux model for the water column of the southern basin:

$$\frac{dC_s}{d_t} = \left[\frac{1}{2}(L_{OF}) + L_{SE} + V_e(C_T - C_S) + X \right] / V_S \quad (4)$$

Where $\frac{dC_s}{d_t}$ is the change through time of nutrient concentration in water of the southern basin; L_{OF} is the loading of sewage plus freshwater nitrogen or phosphorus into the OF sector; this loading (from Table 7) is divided by 2, because about half the time the plume containing materials flows directly into the CE sector without entering the SE sector (Bay Flushing); L_{SE} is sewage plus freshwater loading directly into the SE sector; V_e is the daily water exchange volume between the southern basin and the transition zone. C_T and C_S are the material concentrations in the transition zone and the southern basin; V_s is the volume of the southern basin; X is a nonconservative term representing net material uptake or release within the southern basin.

We earlier indicated that the addition of particulate matter to Kaneohe Bay through storm events could be as much as tenfold larger than the average input of materials by streams. We will use the average stream loading in our mass balance model for two reasons. First, the effects of infrequent, large storms are seen in the bay for only a few days. Second, most of the particulate matter remaining in the bay following a storm falls to the bottom; if this material reenters the water column it can be seen as an upward flux term. Since we are concerned here only with the water column, we treat the sediments as either a source or a sink without regard to changes in nutrient content within the sediment layer itself.

In the steady-state case (i.e., $\frac{dC_s}{d_t} = 0$) equation 4 simplifies:

$$\frac{1}{2}(L_{OF}) + L_{SE} + V_e(C_T - C_S) + X = 0 \quad (5)$$

Table 37 summarizes the equations to calculate the nonconservative total nitrogen and phosphorus fluxes before and after sewage diversion, and Figure 43 graphically represents the results of the calculations. If we assume for the moment that the daily exchange volume between the southern basin and the transition zone is not independently known, then there are four equations but five unknowns (the four nonconservative flux terms plus water exchange volume); we therefore cannot derive an explicit solution for

TABLE 37

SOLUTION OF EQUATION 5 WITH THE NONCONSERVATIVE N AND P FLUX TERMS (X) AND EFFECTIVE NET TIDAL FLUX (V_e) AS UNKNOWNS

NITROGEN	PHOSPHORUS
$X_{N_{pre}} = 23 - V_e \cdot (3.2)$	$X_{P_{pre}} = 2.5 - V_e \cdot (0.42)$
$X_{N_{post}} = 5 - V_e \cdot (1.8)$	$X_{P_{post}} = 0.2 - V_e \cdot (0.18)$

NOTE: There are four equations and five unknowns, therefore no explicit solution.

these equations. However, we can use the previous estimate of tidal exchange and the likely uncertainty to calculate the fluxes.

Tidal exchange between the southern basin and the transition zone totals $6 \times 10^6 m^3 \cdot day^{-1}$ (Bay Flushing). We consider 5 and $7 \times 10^6 m^3 \cdot day^{-1}$ to be the likely extremes of the effective exchange volume (Bay Flushing), and Figure 43 demonstrates that interpretations of nonconservative nutrient fluxes are quantitatively but not qualitatively altered by these extremes. We will therefore use the tidal exchange volume ($6 \times 10^6 m^3 \cdot day^{-1}$) to calculate and discuss various rates within the southern basin.

The cycle observed for phosphorus must be relatively simple, representing a balance between detrital accumulation in the sediments and benthic biomass and subsequent regeneration in the sediments, releasing phosphorus back to the water. During the prediversion period the phosphorus cycle was virtually balanced for the range of V_e (Figure 43); that is, phosphorus accumulation and release were approximately equal. After diversion, regenerative release of phosphorus proceeded more rapidly than accumulation; there was a net loss of phosphorus from the southern basin, over the reasonable range of values for V_e.

It is apparent from Figure 43 that nitrogen was accumulating in the southern basin before sewage diversion and lost from there after diversion. Again, the conclusion holds over the range of V_e. Terms that must be considered in the nitrogen cycle in addition to sedimentation, biological accumulation, and regeneration are nitrogen fixation and denitrification. Nitrogen fixation is a quantitatively important process in some coral reef

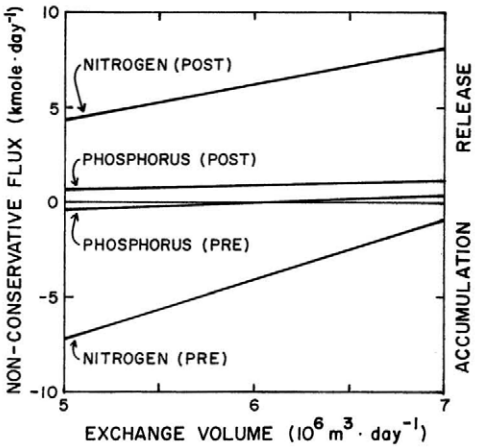


FIGURE 43. Apparent nonconservative nitrogen and phosphorus fluxes in the southern basin as a function of exchange volume. Positive values denote additions of material to the water column.

environments; denitrification is not ordinarily important in the largely aerobic sediments of coral reefs, because it is an anaerobic process (Wiebe 1976, 1979). Data from Hanson and Gundersen (1976) suggest that nitrogen fixation in the southern basin of Kaneohe Bay might have totaled 1 $kmole \cdot day^{-1}$ before sewage diversion. Those authors suggested that denitrification probably was not important, although Elkins (1978) presented evidence that denitrification might occur in deeper, anaerobic portions of lagoon sediments. Before sewage diversion, the sum of these two nitrogen flux terms must have been between 0 and 1 $kmole \cdot day^{-1}$.

In the absence of the large external nitrogen subsidy from sewage, the process of nitrogen fixation probably increased somewhat in importance. Wiebe, Johannes, and Webb (1975) estimated that nitrogen fixation rates on coral reefs can be as high as 15 $mmoles \cdot m^{-2} \cdot day^{-1}$; extrapolated over the reef-flat hard-bottom area of the southern basin (0.7 km^2, Table 16), this rate would yield a postdiversion nitrogen fixation rate of 10 $kmoles \cdot day^{-1}$. We consider it likely that this rate substantially overestimates nitrogen fixation in the southern basin. Because of the likely continuation of denitrification in the sediment, we conclude that the sum of these internal nitrogen fluxes was 0–10

TABLE 38

COMPARISON OF LOADING AND EXPORT FOR SPECIFIC NUTRIENT POOLS IN THE SOUTHERN BASIN (kmoles·day^{-1})

	PREDIVERSION		POSTDIVERSION	
	LOADING	EXPORT	LOADING	EXPORT
Nitrogen				
dissolved inorganic	11	2	3	0
dissolved organic	9	5	1	4
particulate	3	12	1	7
total	23	19	5	11
Phosphorus				
dissolved inorganic	1.9	1.5	0.1	0.3
dissolved organic	0.5	0.2	0.0	0.4
particulate	0.1	0.8	0.1	0.4
total	2.5	2.5	0.2	1.1
Dissolved silicon	20	12	26	20
Particulate organic carbon	21	37	14	26

kmoles·day^{-1} during the postdiversion period. If the ranges for nitrogen fixation are reasonable, then it appears that these processes were probably not important to net nitrogen flux before sewage diversion but may have become important after diversion.

Further insight into the nutrient flux is gained by comparing nutrient loading into the southern basin with net export to the transition zone (Table 38). Both before and after diversion, the major supply of nitrogen was inorganic, while the major export was particulate. This contrasts with phosphorus, for which both the major import and a major export were dissolved. An incomplete budget for dissolved silicon demonstrates that most dissolved silicon delivered to the system was apparently exported in that form. The importance of these calculations is the demonstration that the biological community of the southern basin converts virtually all of the dissolved fixed nitrogen made available by external supply or internal production into particulate nitrogen, whereas other dissolved nutrients critical to autotrophic growth are supplied in excess and exported without total conversion to particulate organic materials. This interpretation is consistent with the conclusions of Caperon (1975), Caperon, Cattell, and Krasnick (1971), Laws and Redalje (1979), and data in the section on metabolism, that nitrogen was the nutrient most limiting to total community metabolic activity in Kaneohe Bay both before and after sewage diversion.

Note that more particulate organic materials (exemplified by carbon, Table 38) were exported from the southern basin than were supplied, a situation that resulted from net organic production in the southern basin. Data from Taguchi (1980) suggest that particulate carbon sedimentation in the southern basin was near 300 kmoles·day^{-1}, so that the net export of 10–20 kmoles·day^{-1} represented only a small fraction of the carbon production there; most of the net carbon production was trapped. The consequence to the ecosystem of this entrapment, or sedimentation, was delivery of particulate organic detritus to the benthos. Benthic response to this sedimentation before diversion was a large macrofauna (and probably also microheterotroph) buildup relative to autotroph buildup (Tables 31 and 35), net heterotrophic metabolism in the reef-flat community before sewage diversion (Kinsey 1979, and Table 43), nutrient regeneration from the sediments and a decrease in that release after diversion (Harrison 1981, and Table 48), and a dramatic decline in the animal population after sewage diversion (Table 34).

The results of these calculations with re-

spect to nutrient cycling may be summarized as follows. In apparent response to sewage diversion, the southern basin of Kaneohe Bay began releasing both nitrogen and phosphorus. The release apparently resulted from a sharp decrease in particulate supply to the benthos, a drop in benthic animal biomass and a consequent decline in the ability of the community to store nutrients in benthic biomass or to use that biomass to transfer nutrients to particulate detritus. Nitrogen fixation may also have accounted for some of the postdiversion nitrogen export.

Water Clarity

Water clarity is sensitive to environmental perturbation and is noticed by the public, as well as being important to the biological functioning of the ecosystem. For these reasons, it is appropriate to examine the role of water clarity in ecosystem dynamics.

Variations in water clarity can arise from three weakly related mechanisms—biotic production, mixing of detritus off the bottom and into the water column by wind, and runoff of particulate materials from land. In the section on Water Composition we concluded that runoff was not significant to the average water-clarity values obtained during this study (although it has a dramatic short-term effect on bay waters); therefore that process will not be considered further.

Figure 30 demonstrates that there is a relatively strong correlation between chlorophyll and water clarity ($r^2 = 0.47$), with a change of 1 $mg \cdot m^{-3}$ in chlorophyll accounting for about a 0.11 m^{-1} change in extinction coefficient. According to Bannister (1974), the relationship between chlorophyll and extinction coefficient based solely on the effect of chlorophyll should only be about 0.016, or 15 percent of the measured value. These calculations suggest that 85 percent of the variation in extinction coefficient is related to light-scattering particles other than chlorophyll but correlated with chlorophyll. Supporting this interpretation is the observation that the coefficient of determination (r^2) between extinction coefficient and total particulate volume is 0.70 (Figure 31). Moreover, according to the calculations in Table 21, only about 20–25 percent of the particulate organic material in the water column is shown to be phytoplankton; most of the remainder is detritus.

The part of the variance in the attenuation or extinction coefficient related to wind speed is due to the stirring of detritus (including both organic and inorganic material) off the bottom into the water column. The fact that chlorophyll itself is not significantly correlated with short-term wind speed (Water Composition) suggests that most of the resuspended material is refractory and takes little part in nutrient cycling. The refractory nature of this resuspended material is further demonstrated by the increase in percent ash in microplankton samples with increasing wind.

Release of nutrients from the sediments is a significant part of the nutrient cycle within Kaneohe Bay (Lagoon-Floor Community Metabolism) and must therefore contribute to chlorophyll. The fact that chlorophyll is not correlated with short-term wind speed suggests that there is sufficient turbulence to keep dissolved materials vertically homogenous in the water column, despite the heterogeneity that develops in particulate materials during calm periods (Figure 32).

Benthic plants are potentially particularly sensitive to this variation in water clarity, because their photosynthetic ability is directly tied to available light. The specific phenomenon of light limitation of benthic metabolism is investigated further elsewhere (see *Dictyosphaeria cavernosa* Metabolism), but Table 39 serves as an introduction to this point. The light intensity (I_z) reaching some depth (Z) can be calculated from the surface intensity (I_o) and extinction coefficient (k):

$$I_z = I_o e^{-kz} \qquad (6)$$

The depth to which 1 percent of ambient light penetrates and the percentage of light penetration to a depth of 1.5 m are useful indices to put the extinction coefficient into biologically relevant perspective. The average depth to which 1 percent of the ambient light penetrates in each sector is taken as an index of the maximum depth of net photosynthetic activity (i.e., the base of the photic zone). The lagoon floor, with a mean depth

TABLE 39

REPRESENTATIVE CHARACTERISTICS OF LIGHT DISTRIBUTION IN KANEOHE BAY

	NW	CE	SE	OF
Depth of 1 percent light (m)				
pre	17	18	14	8
post	21	20	17	12
Δ	+4	+2	+3	+4
Ambient light at 1.5 m (percent)				
pre	64	66	60	39
post	71	69	75	54
Δ	+7	+3	+15	+15

of about 15 m, was well below the photic zone at OF before sewage diversion and marginally below after diversion. SE was marginal before diversion, but in other cases both before and after diversion, the lagoon floor of Kaneohe Bay lay within the photic zone.

The deepest parts of the reef flats (with rare, local exceptions) are about 1.5 m below mean sea level. This depth in the OF sector before sewage diversion received less than 40 percent of ambient light. After diversion the light received at the base of the reef flat rose above 50 percent, whereas the reef flats of other sectors received more than 60 percent light both before and after sewage diversion. It follows from these measurements that light available to the benthos for photosynthetic activity was substantially lessened near the outfall in the presence of sewage and the particulate materials that were produced. This condition was changed by sewage diversion, apparently back to approximately the conditions that prevailed before sewage was discharged into the bay.

Metabolism

Biotic components of the bay were previously shown to have changed since sewage diversion (Biotic Composition). In the section on Nutrient Cycling in the Southern Basin we considered the changing mass balance of nutrients within the ecosystem and isolated components of nutrient flux apparently attributable to internal sources and sinks, and suggested that biological processes probably accounted for most of the internal changes. In this section we consider selected biological processes within the ecosystem and evaluate how the sewage and its diversion appear to have affected biological activity within the bay.

Altered biological activity can be recognized from changing community composition and biomass or from altered biological processing of oxygen, carbon, nitrogen, or phosphorus. Any of these changes reflects altered metabolism, either at the level of the entire community or at the level of individual organisms. Any such change is here termed a metabolic change.

Two distinct classes of metabolic response to the sewage can occur—stimulation of metabolism because of fertilization, and inhibition of metabolism through toxicity, oxygen depletion, or other causes. We have found no evidence of direct toxic inhibition by sewage, and oxygen levels have remained high enough to preclude oxygen inhibition. We have observed other inhibitive effects. Both stimulatory and inhibitive effects are documented in the case histories that follow.

PHYTOPLANKTON METABOLISM: The most conspicuous and immediate biological response to the discharge and diversion of sewage occurred with respect to the phytoplankton. The phytoplankton community built up rapidly, as shown by chlorophyll increases, when significant sewage discharge began in the OF sector (Piyakarnchana 1965; Figure 26), and the chlorophyll-rich plume virtually disappeared when the discharge ceased (Figure 25). Availability of nutrients is the most obvious variable of interest in this regard, with two questions to consider: What is the specific role of nutrients in affecting the phytoplankton? Which nutrient most significantly affects the phytoplankton?

Table 40 summarizes variables of primary relevance to phytoplankton biomass and metabolism. First consider the hourly photosynthetic rates. Laws and Redalje (1979) found that mean dawn-to-dusk productivities were approximately 8.4 times the measured hourly rates; they then adjusted

TABLE 40

BIOMASS, PRODUCTION, AND NUTRIENT ASSIMILATION RATES OF PHYTOPLANKTON IN KANEOHE BAY

SECTOR AND VOLUME ($10^6 m^3$)	OF 5.35	SE 74.24	CE 119.68	NW 66.41	BAY TOTAL 265.68
Net production ($mgC \cdot m^{-3} \cdot day^{-1}$)					
pre	294	78	38	36	54
post	54	31	20	23	25
Biomass ($mgC \cdot m^{-3}$)					
pre	220	89	36	31	53
post	69	54	27	26	35
Growth rate (day^{-1})					
pre	1.34	0.88	1.06	1.16	1.02
post	0.78	0.57	0.74	0.88	0.71
Phyto. nitrogen standing crop (kmoles)					
pre	15	83	54	26	178
post	5	50	41	22	118
Phyto. phosphorus standing crop (kmoles)					
pre	0.9	5.2	3.4	1.6	11.1
post	0.3	3.2	2.5	1.4	7.4
Nitrogen assimilation ($kmoles \cdot day^{-1}$)					
pre	20	73	57	30	180
post	4	29	30	19	82
Phosphorus assimilation ($kmoles \cdot day^{-1}$)					
pre	1.2	4.6	3.6	1.9	11.3
post	0.2	1.8	1.9	1.2	5.1

these daytime rates downward by 15 percent (following Steemann-Nielsen and Hansen 1959) to account for nighttime respiration in order to estimate 24-hour net production rates. It is further possible to estimate the approximate phytoplankton biomass by assuming a carbon-to-chlorophyll mass ratio of 50 : 1 (Biotic Composition). The daily growth rate of the phytoplankton can then be approximated as the net productivity divided by biomass. Finally, the magnitude of net nitrogen and phosphorus assimilation can be approximated by the C : N : P molar ratio of 106 : 16 : 1 (Redfield, Ketchum, and Richards 1963). The validity of applying this ratio to particulate materials in Kaneohe Bay can be defended by a consideration of Figure 23 and Tables 8 and 10. The figure shows a 16 : 1 slope for a regression of particulate nitrogen versus phosphorus; the tables show an average C : N ratio between 5 and 8 for particulate organic materials in the bay. Thus particulate materials in the water column approximate the Redfield ratio.

Maximum growth rates reported for phytoplankton are quite variable, depending on both temperature and the characteristics of individual species. Eppley (1972) examined the growth rate of a large number of unicellular laboratory cultures as a function of temperature and concluded that the maximum growth rate at 25° C (about the temperature of Kaneohe Bay) under optimal light and nutrient conditions was about $2.9 \cdot day^{-1}$. However, Laws and Bannister (1980) noted that there are significant interphyletic differences among the phytoplankton. At 25° C, chlorophytes tend to have the highest growth rates ($2.5–3.0 \cdot day^{-1}$), followed by diatoms ($1.5–2.0 \cdot day^{-1}$) and dinoflagellates ($0.3–0.8 \cdot day^{-1}$) (Chan 1978; Laws and Bannister 1980). The phytoplankton community of Kaneohe Bay is composed primarily of diatoms and secondarily of dinoflagellates, with few chlorophytes, so that the prediversion growth rates ($0.9–1.3 \cdot day^{-1}$) are probably in the range of 50–100 percent of the maximum growth rate which might be expected for this community. In apparent response to the diversion, the growth rate dropped by about 30 percent. This conclusion is based on the assumption

that the carbon-to-chlorophyll ratio remained nearly constant.

The effect of nutrient addition on the phytoplankton can be addressed by comparing assimilation rates in Table 40 with the N and P loading rates (Table 7). Ratios of N and P loading to assimilation were 0.12 and 0.33, respectively, before sewage diversion, decreasing to 0.09 and 0.05 after diversion. Thus most of the nutrient uptake was supported by recycling, both within the water column and from the benthos. Caperon (1975) also noted that such cycling was the major proximate source of nitrogen to support phytoplankton productivity.

Phytoplankton biomass decreased following sewage diversion by 16, 25, 39, and 59 percent, respectively, at stations NW, CE, SE, and OF. Growth rates declined by comparable amounts, respectively, 24, 30, 35, and 42 percent. The decreases in dissolved inorganic nitrogen at the four stations were also of the same magnitude, except at NW. The effects of dissolved nutrient loading on growth rate must have been indirect because most of the nutrient taken up by phytoplankton was recycled. Evidently the high nutrient loading maintained a high standing stock of particulate matter, which resulted in high recycling rates in the water column. In addition, as we shall see below, the benthic remineralization rate was also enhanced before sewage diversion, apparently because of an enhanced sedimentation rate.

The proportion of uptake directly supported by nutrient loading decreased after sewage diversion, suggesting that the capacity of the system to utilize the average dissolved nutrient concentration was exceeded somewhat during the prediversion period. The prediversion export of dissolved inorganic nutrients, especially phosphorus (Table 38), also supports this conclusion. Nevertheless, the magnitude of the decrease in particulate nitrogen was much larger and more consistent than that in dissolved inorganic nitrogen.

Nitrogen and phosphorus are the nutrients most likely to limit phytoplankton biomass in aquatic ecosystems, with nitrogen the more likely limiting nutrient in marine systems (Ryther and Dunstan 1971) and phosphorus more likely limiting in freshwater (Schindler 1977). Since sewage contains a nitrogen-to-phosphorus ratio that is low relative to the nutritional needs of phytoplankton (Ryther and Dunstan 1971), it is almost invariably the case that nitrogen is the first nutrient to limit phytoplankton biomass in marine ecosystems receiving sewage.

During both prediversion and postdiversion conditions, we performed a series of nutrient enrichment experiments at both the SE and NW stations to learn whether nitrogen or phosphorus was the more limiting nutrient. Details of the experimental procedure are given in Laws and Redalje (1979), with prediversion results. Here we summarize the procedure and report both prediversion and postdiversion results. Water was prescreened through 102-μm mesh and 500-ml aliquots were incubated under appropriate light and temperature conditions for 2–3 weeks. Chlorophyll-*a* was measured every 2–3 days, and the maximum concentration achieved during the incubation was taken to be the yield for that incubation. In each experiment, one incubation flask served as a control and received no nutrient addition; a second flask received a standard addition of essential nutrients (including trace metals) except nitrogen; a third received all nutrients except phosphorus. This approach to analyzing nutrient enrichment experiments avoids the problems associated with short-term ^{14}C bioassays, as discussed by Gerhart and Likens (1975). The results are shown graphically in Figure 44.

The results reveal no significant difference (t test, $p > 0.05$) in the yields from the unenriched control flasks and the flasks lacking nitrogen. Both before and after diversion, the flasks receiving nitrogen but lacking phosphorus yielded more chlorophyll than the controls. These results demonstrate that nitrogen was limiting phytoplankton biomass in Kaneohe Bay and that phosphorus was not limiting.

Perry (1972) and others have reported that phosphorus is limiting if alkaline phos-

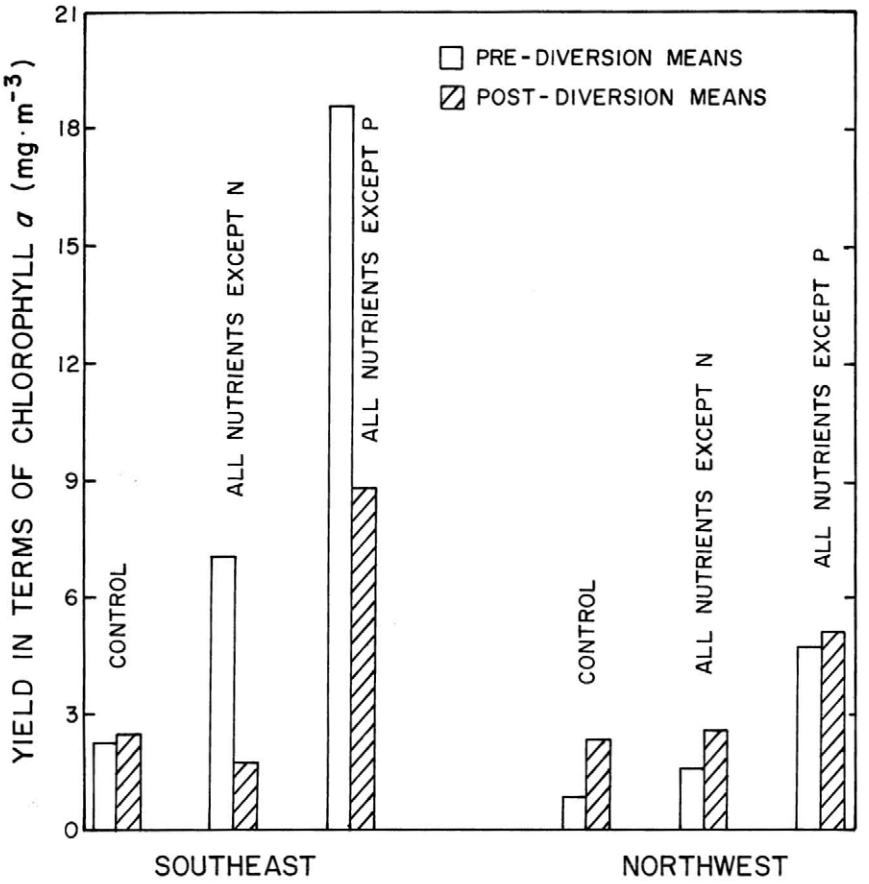


FIGURE 44. Nutrient enrichment yield results.

phatase activity can be detected in the water. After sewage diversion, we checked on ten occasions for alkaline phosphatase activity and noted it only once. This observation further indicates that phosphorus was not limiting.

As a third consideration of nitrogen versus phosphorus limitation, we repeatedly measured inorganic phosphorus and inorganic nitrogen along a transect between the OF and SE stations before sewage diversion. Figure 45 demonstrates that inorganic nitrogen was depleted more rapidly than inorganic phosphate. The graph indicates residual phosphate when the nitrogen was exhausted. We thus conclude that in the presence of sewage input to the bay, nitrogen was the nutrient limiting biomass of phytoplankton; this remained the case after sewage diversion, under a much lower nitrogen and phosphorus loading regime.

Because the amount of loading controls biomass, the phytoplankton biomass has dropped. The fact that nitrogen washout exceeded loading after sewage diversion (Table 38) probably reflects the loss of nitrogen from benthic compartments (biomass, sediments) after sewage diversion. As previously discussed, there may also now be significant nitrogen fixation in the southern basin.

ZOOPLANKTON METABOLISM: It was demonstrated in the previous discussion that

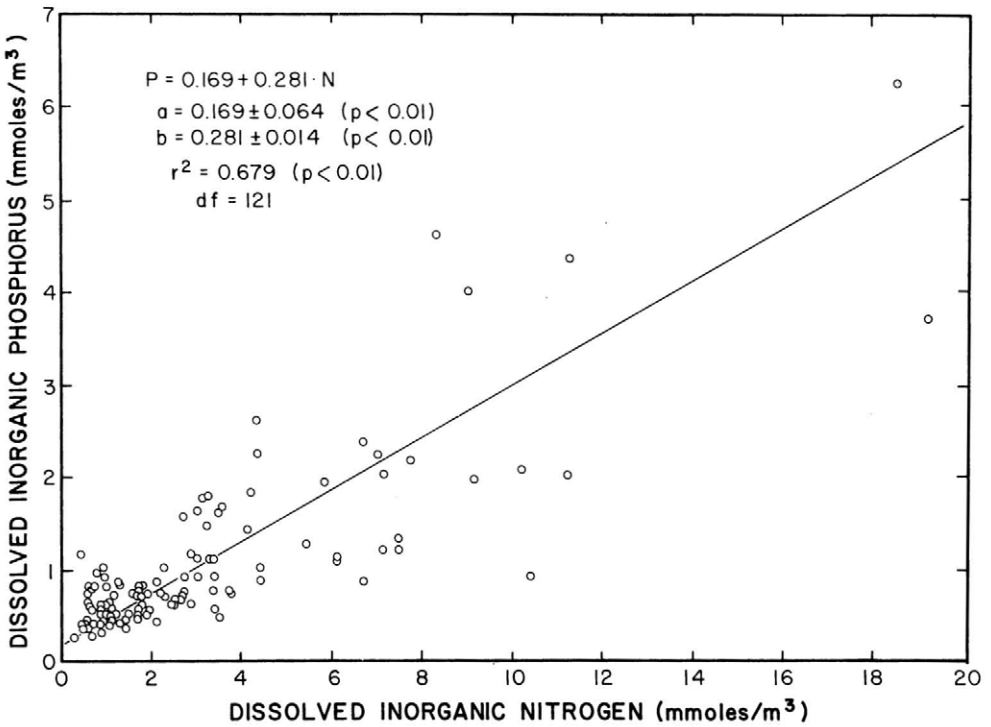


FIGURE 45. Dissolved inorganic nitrogen and phosphorus in the vicinity of the OF station.

nutrient loading into the southern basin was, by a large shortfall, insufficient to account for nutrient uptake by the phytoplankton there. In this section we consider the contribution of zooplankton metabolism to the nutrient turnover that must occur within the ecosystem to support total community metabolism.

We estimated the biomass in each of several taxonomic and size classes from the count data, from biomass estimates based on size, and from literature values for biomass per animal (Bartholomew 1973; Hirota and Szyper 1976; Kimmerer 1980; Peterson 1975). Mean biomass in each sector was close to the means in Tables 25 and 26. We then used the size-specific biomass data to compute metabolic rates as described below.

Specific excretion rates are a function of the size of the organism. We used the relationship of body-equivalent excretion time (BEET) to body size, as presented by Johannes (1964) for phosphorus, to derive this function. If it is assumed that nitrogen excretion has the same slope with body size as phosphorus, then the specific nitrogen excretion rate ($BEET^{-1}$) is proportional to $N^{-0.33}$, where N is body nitrogen. To estimate the proportionality constant, we used data for total nitrogen excretion rates of macrozooplankton in Kaneohe Bay (Szyper et al. 1976). We used only data from samples taken by plankton seine, because the net-caught samples had higher excretion rates, probably indicating stress (Szyper et al. 1976). We calculated the mean nitrogen per animal from count data for these same samples and determined an expression for nitrogen specific excretion rate as:

$$BEET^{-1} = 0.3\ N^{-0.33} \qquad (7)$$

Data on respiration rates for plankton are neither as complete nor as convincing as those for excretion, and there are few data on microplankton respiration. The ratio of $C_{respired}$: $N_{excreted}$ (C_r : N_x), neglecting excre-

TABLE 41

ESTIMATES OF RESPIRATION, EXCRETION, AND TURNOVER FROM MACRO- AND MICROZOOPLANKTON

	MACROPLANKTON						MICROPLANKTON					
STATION	R	CT	NE	NT	PE	PT	R	CT	NE	NT	PE	PT
NW												
pre	1.0	0.4	0.2	0.25	0.03	0.6	8	1.2	1.6	0.8	0.2	2.0
post	1.0	0.4	0.2	0.25	0.03	0.6	9	1.2	1.8	0.8	0.3	2.0
CE												
pre	2.5	0.4	0.5	0.25	0.08	0.6	26	1.4	5.3	0.9	0.8	2.2
post	1.5	0.4	0.3	0.25	0.05	0.6	18	1.4	3.6	0.9	0.6	2.2
SE												
pre	8.5	0.4	1.7	0.25	0.27	0.6	44	1.4	8.9	0.9	1.4	2.2
post	5.0	0.4	1.0	0.25	0.16	0.6	34	1.5	6.8	1.0	1.1	2.5
OF												
pre	9.5	0.4	1.9	0.25	0.30	0.6	60	1.5	12.0	1.0	1.9	2.5
post	4.5	0.4	0.9	0.25	0.14	0.6	40	1.5	8.1	1.0	1.3	2.5

NOTE: R = Respiration ($mgC \cdot m^{-3} \cdot d^{-1}$); CT = Carbon turnover (d^{-1}); NE = Nitrogen excretion ($mgN \cdot m^{-3} \cdot d^{-1}$); NT = Nitrogen turnover (d^{-1}); PE = Phosphorus excretion ($mgP \cdot m^{-3} \cdot d^{-1}$); and PT = Phosphorus turnover (d^{-1}).

tion of dissolved organic carbon, depends upon the C : N ratio of food, feces, and growth, as well as on assimilation and net growth efficiency. If the assimilation efficiency is high or if the C : N ratio of food and feces is about the same, then the $C_r : N_x$ should be close to that of the food. Assuming this to be true, we have used a $C_r : N_x$ value of 6 (i.e., close to the Redfield ratio, as discussed for phytoplankton).

Turnover of phosphorus is usually faster than that of nitrogen. For example, Szyper et al. (1976) estimated phosphorus specific excretion rates about three times those they reported for nitrogen. Ratios summarized by Corner and Davies (1971) are around 2 to 2.5. We used a ratio of 2.5 and assumed an atomic N : P ratio in the zooplankton of 16 (i.e., the Redfield ratio) resulting in phosphorus excretion rates about 0.16 times (by weight) those of nitrogen.

Table 41 shows values calculated for biomass, nitrogen and phosphorus excretion, respiration, and turnover of carbon, nitrogen, and phosphorus. Our turnover rates for macroplankton nitrogen are $0.25 \cdot day^{-1}$, close to the value of $0.26 \cdot day^{-1}$ calculated by Szyper et al. (1976). About half the excreted nitrogen may be urea (Szyper et al. 1976), which is apparently about as readily available for phytoplankton uptake as is recycled inorganic nitrogen (Eppley et al. 1973; McCarthy 1972; Webb and Haas 1976). Our macroplankton phosphorus turnover rates are about $0.6 \cdot day^{-1}$, while Szyper et al. (1976) reported about $0.9 \cdot day^{-1}$. Our calculated turnover rates for microplankton nitrogen are 0.8 to $1.0 \cdot day^{-1}$, about twice the rate reported by Caperon et al. (1979) for ammonium excretion using a ^{15}N isotope dilution technique. We assume that the difference can be accounted for by urea excretion, as discussed above for macroplankton. While we did not estimate the nutrient turnover of nekton, we expect it to be insignificant compared to that of zooplankton.

These nutrient excretion rates allow us to estimate the prediversion and postdiversion nutrient release rates attributable to zooplankton in the southern basin (Table 42). Before sewage diversion, the zooplankton apparently excreted about 62 kmoles $N \cdot day^{-1}$ and 4.4 kmoles $P \cdot day^{-1}$; these figures dropped by approximately 25 percent with sewage diversion. These numbers must be regarded as no more than a rough approximation of the role of zooplankton in nutrient cycling within the bay. The calculations exclude plankton smaller than 35 μm, which may contribute about half of the total excretion (Caperon et al. 1979). However some of the nutrient cycling within that pool may

TABLE 42

ESTIMATED ZOOPLANKTON N AND P EXCRETION RATES IN THE SOUTHERN BASIN (kmoles·day^{-1})

	NITROGEN EXCRETION	PHOSPHORUS EXCRETION
Prediversion	62	4.4
Postdiversion	45	3.3

be implicit within the phytoplankton nutrient uptake estimates. Moreover, the calculations assume that the specific excretion rates were unaffected by the reduced food supply after sewage diversion. Before sewage diversion the estimated zooplankton excretion accounted for about 70 percent of the nitrogen uptake and 80 percent of phosphorus uptake (Table 40). Following sewage diversion both excretion estimates exceeded uptake; this suggests that specific excretion rates may have decreased after diversion.

REFF-FLAT COMMUNITY METABOLISM: Shallow reef communities are known to be metabolically very active (see Kinsey 1979; Kinsey and Domm 1974; Smith 1974; Sournia 1977 for recent reviews of this topic), and reef flats comprise approximately one-third of the area of inner Kaneohe Bay (Table 2). Reefs can maintain high metabolic activity in nutrient-poor waters (Johannes et al. 1972); apparently this high activity is made possible by a near balance between gross organic carbon production and respiration. The communities appear to be able to match any phosphorus losses by uptake (Pilson and Betzer 1973; Smith and Jokiel 1978), and nitrogen losses (Wiebe, Johannes, and Webb 1975) appear to be balanced by fixation of atmospheric nitrogen (Webb et al. 1975). In the face of this "standard reef performance" in low-nutrient waters, we have examined the Kaneohe Bay reefs, which have been subjected to high loading of nutrients (especially particulate nutrients). Comparison of Kaneohe Bay reef metabolism with "standard reef performance" was a major topic of the dissertation by Kinsey (1979). Relevant results of that investigation are summarized here.

Kinsey adapted the techniques described elsewhere (Kinsey 1978; Smith and Kinsey 1978) to estimate organic carbon production and consumption and calcium carbonate production from oxygen, pH, and alkalinity changes of water flowing across the reef flats.

Figure 36 shows the locations of reef-flat transects for five sites in the bay. In the southern basin two sites in addition to the standard OF benthos transect site were used. The Coconut Island site (CI) was relatively exposed to SE sector nutrient pollution but was effectively out of the influence of streams. As such, it approximated a response to a water composition nearer that of the SE sector station than that of the OF sector (Water Composition). The Lilipuna Reef site (LR) is in the frontal flow identified in the discussion of Bay Flushing, hence directly in the sewage plume about half of the time. This station was established after the frontal flow from the vicinity of the sewer outfall along the shoreline had been documented.

Table 43 presents the organic carbon production and respiration data for the sites. These data have been seasonally weighted and corrected for planktonic production at the sites (Kinsey 1979). The data from the CI and OF stations in the southern basin have been averaged; the LR station is informative, but is assumed to represent a negligible fraction of the southern basin.

Production showed only a 40-percent variation from one end of the bay to the other, whereas respiration doubled from NW to SE. Kinsey (1979) considered the pattern in more detail. Of particular importance to this study and internally rather consistent was the relationship between gross production and respiration, which may be expressed as a ratio that on most coral reefs is very near 1.0, or as the difference between production and respiration (usually near 0.0).

SE sector reefs consumed far more organic carbon than they produced before sewage diversion, leading to a net carbon deficit averaging 1.4 gC·m^{-2}·day^{-1} and a production to respiration ratio near 0.7. This pattern shifted toward net autotrophy ($P/R > 1.0$) farther north in the bay. The heterotrophic stimulation by the sewage was

TABLE 43

REEF-FLAT COMMUNITY ORGANIC METABOLISM FOR TRANSECTS IN THE BAY

TRANSECT	AREA ($10^6 m^2$)	PRODUCTION ($gC \cdot m^{-2} \cdot day^{-1}$)	RESPIRATION ($gC \cdot m^{-2} \cdot day^{-1}$)	P − R	$\frac{P}{R}$
NW	5.53	4.1	2.3	1.8	1.78
CE	3.40	5.2	4.5	0.7	1.16
CI	—	3.8	5.3	−1.5	0.72
LR	—	5.2	12.7	−7.5	0.41
SE/OF	—	3.3	4.6	−1.3	0.72
Southern basin average*	1.57	3.6	5.0	−1.4	0.72
Bay Total*	10.50	4.4	3.4	1.0	1.29

SOURCE: Kinsey (1979).
*Excludes LR data.

most evident at the LR site, directly in the sewage plume.

Consistent with these metabolic observations is the further observation (Figure 39, Table 34) that benthic animal biomass was highest at the OF site. This heterotrophic weighting toward the OF sector would perhaps have been even greater if the substrata had not deteriorated due to siltation, dredging, and bioerosion. It is often the case that sewage loading leads to increased animal biomass; diversity may go up or down, depending upon specific conditions governing the loading (e.g., Dauer and Conner 1980). These authors claimed not to know the specific functional pathway by which sewage stimulated the biomass buildup, although they recognized that somewhere the transformation of sewage to organic materials accounted for the buildup. We hypothesized that the heterotrophic biomass buildup of the SE sector hard bottom was simply stimulated by the planktonic particulate organic production and detrital fallout on the reef-flat biota. We used the microcosm tanks at Coconut Island (described by Smith et al. 1979) to test this hypothesis.

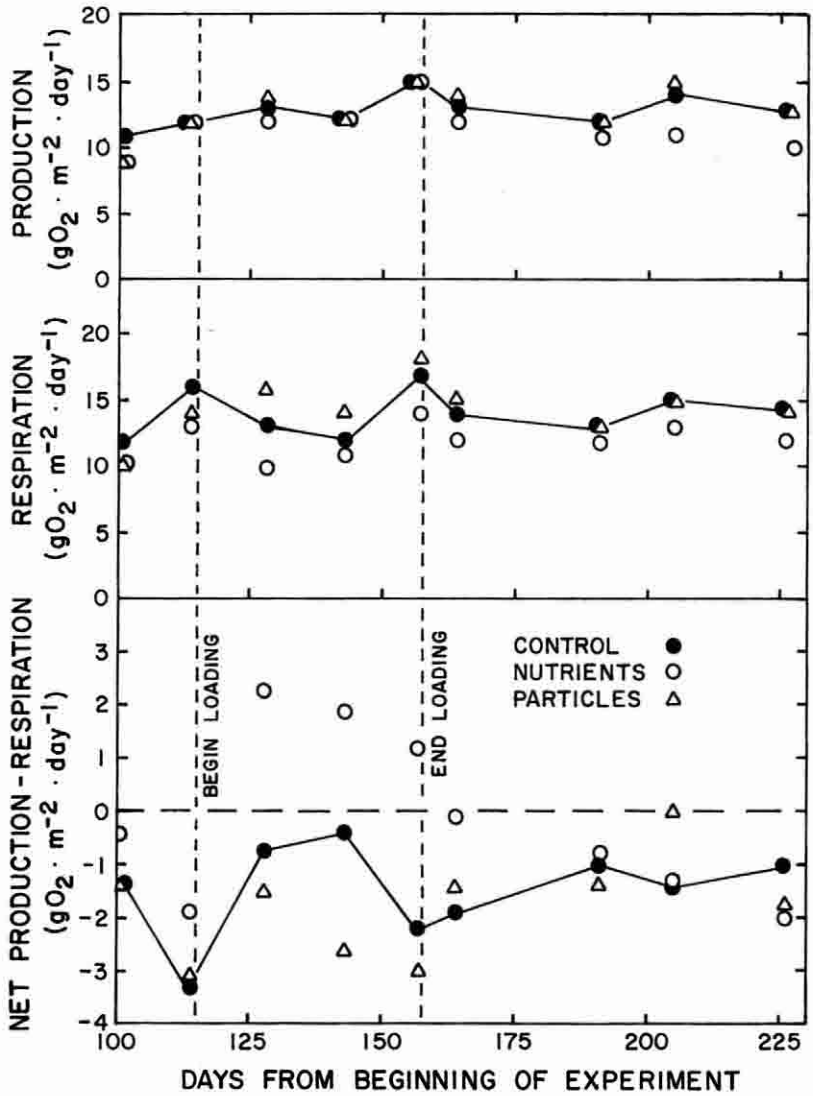
The experiment was performed in early 1978, after both particulate and dissolved nutrient concentrations of the southern basin intake water for the microcosms had dropped below prediversion levels. Reef-flat communities from the reef crest of the OF sector were transported to the microcosm tanks and allowed to stabilize for $3\frac{1}{2}$ months in each of six microcosm communities. Then two tanks were maintained as controls; two received a loading of dissolved inorganic nutrients (0.1 mole $N \cdot day^{-1}$; 0.01 mole $P \cdot day^{-1}$); and two received the equivalent N and P loadings in the form of particulate organic material. Bakers' yeast was used as an inert particulate organic material source.

Figure 46 summarizes the results. Addition of particulate organic materials shifted the microcosm communities toward net heterotrophy in increasing respiration. The system was rapidly responsive to termination of particle loading, with production minus respiration converging on the control as soon as particle loading was terminated.

Inorganic nutrient addition also elicited a community response. The communities receiving inorganic nutrients became autotrophic and remained so until the nutrient loading was terminated. Again, the community response to termination was rapid.

These data suggest that the benthic hard-bottom communities are limited by a variety of resources, including both dissolved and particulate materials; the community metabolism will shift its trophic state rather rapidly in response to altered loading. At least in the case of the microcosm communities, the benthos did not appear to store a large reservoir of either dissolved or particulate materials to use once the external nutritional subsidies were terminated.

It is useful to consider the implications of reef-flat community metabolism to inorganic



FIGURES 46. Production, respiration, and net production minus respiration for reef-flat microcosm communities. The two vertical lines on each diagram represent the onset and termination of particulate and dissolved nutrient delivery to the communities.

nutrient flux in the southern basin. In the section on Biotic Composition we pointed out that the C : N : P ratios of benthic plants and animals differ substantially from the Redfield ratio. We assume that most benthic plant material produced in the southern basin is consumed there, but that the carbon, nitrogen, and phosphorus required to balance the excess of respiration over production must be derived from the water-column particulate load. Results of calculations based on these assumptions and a net carbon respiration of 183 kmoles·day^{-1} for the southern basin (Table 43) yield a nitrogen release of 28 kmoles·day^{-1} and a phosphorus release of 2 kmoles·day^{-1}. These rates are about half the rate of zooplankton release back to the water (Table 42) and

TABLE 44

$CaCO_3$ PRODUCTION RATE FOR REEF-FLAT COMMUNITIES IN KANEOHE BAY
($Kg\ CaCO_3 \cdot m^{-2} \cdot yr^{-1}$)

TRANSECT	$CaCO_3$ PRODUCTION
NW	0.0
CE	8.9
CI	2.4
LR	3.1
OF	−6.5

about 30 percent of the prediversion phytoplankton uptake requirements (Table 40).

The excessive autotrophy in the NW sector (Table 43) probably resulted from a combination of two factors, both related to streams. First, nutrient delivery across shallow water by streams was most immediately available to benthic algae; they could grow in the shallow water and maintain high biomass without washout even with a relatively sporadic nutrient supply. Second, while there was sufficient hard substratum for algal growth, there was neither sufficient substratum nor a sufficiently regular particulate input to favor a high biomass of benthic animals.

Yet one other community metabolic process is noteworthy on the reef flats: the production of calcium carbonate. This process, of course, largely distinguishes coral reefs from many other benthic communities. Data from Kinsey (1979) demonstrate that $CaCO_3$ production occurred throughout most of Kaneohe Bay (Table 44). Freshwater runoff and siltation are assumed to account for the depressed production in the NW sector, but the high net chemical erosion of $CaCO_3$ at the OF station is of particular interest. At this station there was a high biomass of organisms that erode the reef limestone. This observation is consistent with the analyses by White (1980). Even though organic carbon metabolism of the LR and CI sites had shifted toward extreme heterotrophy, those sites were not yet experiencing the high biochemical erosion that characterized the OF site. It is clear that this phenomenon was not an analytical artifact; evidence of reef deterioration at the OF site could be found with only casual inspection. Apparently particulate organic loading and buildup of benthic heterotrophs in shallow tropical waters eventually favor the growth of organisms capable of rapid $CaCO_3$ erosion, hence coral reef destruction. These bioeroding organisms especially include polychaetes and sponges in many reef systems (e.g., Hein and Risk 1975), with the polychaetes being particularly important in Kaneohe Bay (White 1980).

It was demonstrated (Brock and Smith, submitted; also Biotic Composition) that suitable substratum partly limited the buildup of benthic animal biomass in the bay. This erosion, which gradually reduced hard bottom to rubble and eventually to sand, resulted in a long-term inhibition of heterotrophic biomass buildup. The high respiration rate at the LR site, relative to respiration at the OF site (Table 43), is assumed to have represented the greater deterioration of reef substratum from both erosion and siltation at OF.

Dictyosphaeria cavernosa METABOLISM: Various authors (Banner 1974; Banner and Bailey 1970; Maragos 1972; Soegiarto 1973) noted the increase of the so-called green bubble algae in the central portion of the bay. About 1963–1964, the alga began increasing from an ubiquitous but minor component to dominance of the CE sector (Bosch 1967). The favored location was the reef slopes, where the alga competed with, overgrew, and eventually killed *Porites compressa* and other corals of the reef slope. Indeed, this alga dominated the benthic biomass of Kaneohe Bay before sewage diversion (Biotic Composition).

Figure 47 compares the distribution of *Dictyosphaeria* in 1970 with that in 1977, immediately before sewage diversion. Both the northern and southern boundaries of the alga shifted to the north over that period. It has been assumed that the spread of *Dictyosphaeria* was in response to the elevated nutrient loading from sewage, but this explanation was not entirely consistent with the observed migration of the alga's boundaries or its absence from the southern

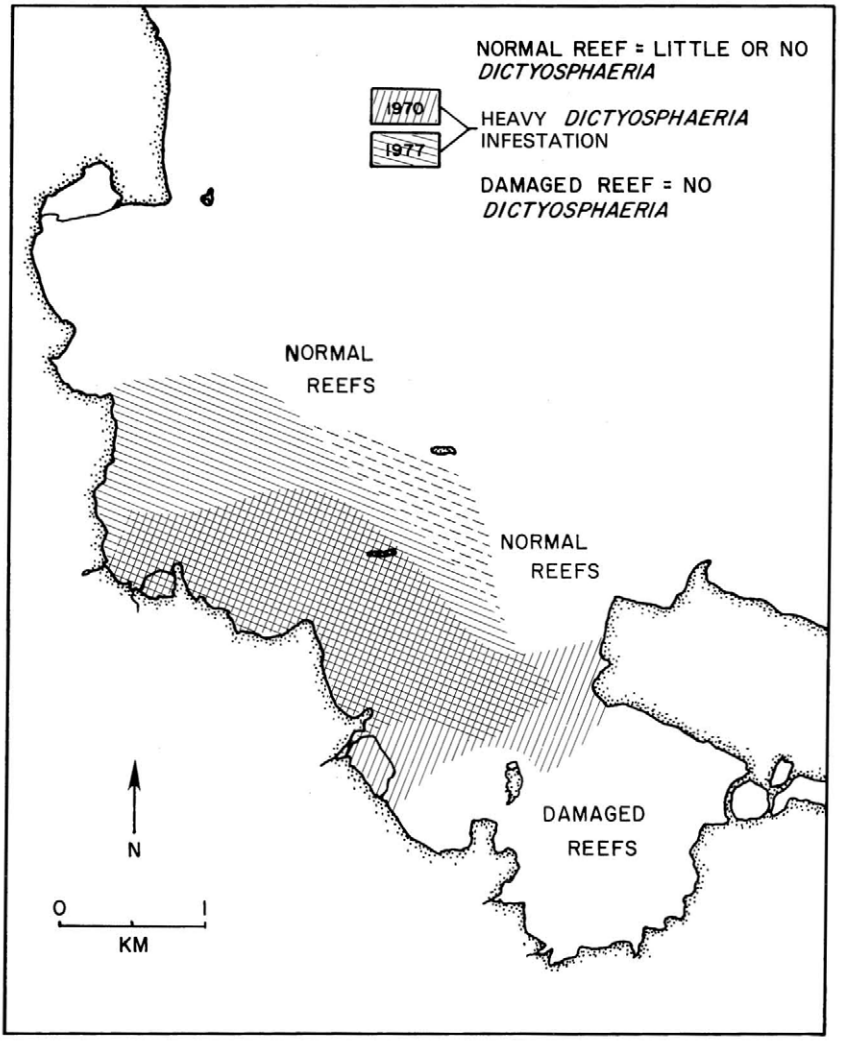


FIGURE 47. Region of maximum *Dictyosphaeria cavernosa* abundance in 1970 and 1977. The 1970 map is adapted from Banner and Bailey (1970).

basin. We attempted to resolve this question with both field sampling and laboratory experimentation.

The biomass of *Dictyosphaeria* on the reef slope and crest was measured during the course of this investigation (Figure 38, Table 30). The biomass and the percent cover showed a substantial variation with time. Diversion occurred while the *Dictyosphaeria* cover was low, and the alga did not recover its prediversion abundance in the following year. It cannot be ascertained from the data how the biomass might have adjusted from a higher seasonal value in response to sewage diversion.

This depressed standing crop accounted for more than 75 percent of the decrease in calculated algal biomass in the bay and appeared to substantiate the notion that the spread of *Dictyosphaeria* had been in response to the sewage. However, the observation still did not explain the absence of *Dictyosphaeria* from the southern basin.

It was our hypothesis that the abundance

TABLE 45

NUTRIENT INCREASES IN FLOW-THROUGH MICROCOSM DURING *Dictyosphaeria* COMMUNITY MICROCOSM EXPERIMENTS

	ULUPAU			COCONUT ISLAND		
	$\mu moles \cdot m^{-2} \cdot hr^{-1}$	± 95%	*N*	$\mu moles \cdot m^{-2} \cdot hr^{-1}$	± 95%	*N*
NH_4	52	± 59	90	221	± 57	108
NO_3	41	+ 57	90	204	± 27	108
PO_4	2	± 17	89	36	± 29	108

NOTE: Because the light and nutrient treatments showed no significant differences, the data have been pooled within sites. The Ulupau facility received clean oceanic seawater poor in nutrients, while the Coconut Island facility received nutrient-rich water from Kaneohe Bay.

of *Dictyosphaeria* and its southern extent were largely limited by light levels needed to sustain growth above community respiration. Benthic microcosm facilities described by Henderson, Smith, and Evans (1976) and Smith et al. (1979) were used to test this hypothesis.

Sections of the *Dictyosphaeria* community were dislodged from the substrata on the reef and transplanted into 1.4 m^2 microcosms. Nine microcosm communities were established at the Coconut Island facility, where they received water rich in particulate and dissolved nutrients from Kaneohe Bay. Six microcosm communities at Ulupau Head received relatively clean open-coast water.

At Coconut Island a 3 × 3 matrix of light and nutrient loading was established. At Ulupau a 2 × 3 matrix of light and nutrients was used. At each facility one row of tanks received 100 percent of ambient sunlight, one received 40 percent, and one received 15 percent. Two levels of ammonium enrichment (+1 and +3 $\mu mole \cdot liter^{-1}$) were maintained at Conconut Island for 30 days with no effect. One level of ammonium enrichment (+1 $\mu mole \cdot liter^{-1}$) was maintained for 81 days at Ulupau. Water flow through the microcosms was approximately 500 $liters \cdot hr^{-1}$, so that the low and high nutrient loading rates were equivalent to 400 and 1200 $\mu moles \cdot m^{-2} \cdot hr^{-1}$, respectively.

There was no evidence from inspection of the data that either the light or the nutrient treatments affected net nutrient flux between the microcosm inlets and outlets. The data were therefore pooled by location. Table 45 demonstrates that the Ulupau communities showed insignificant net nutrient flux, whereas the Conconut Island communities were exporting substantial amounts of both nitrogen and phosphorus. The average net inorganic nitrogen export from the Conconut Island microcosm communities approximately equalled the low-nutrient loading rate. Clearly, the communities were not deriving significant net nutrition from the dissolved nutrient load.

We examined the community structure at the end of the experiment and determined that at Conconut Island, filter feeders were both a large fraction of the biomass and abundant in absolute biomass (Table 46). We therefore examined the nutrient excretion rate of *Ascidia interrupta*, a common tunicate that was abundant in the tanks. Mean excretion rates of nitrogen and phosphorus ($\mu moles \cdot kg\ (wet)^{-1} \cdot hr^{-1}$) were 146 and 2.6, respectively. Since the mean tunicate biomass in the Coconut Island tanks was 770 g, tunicate nitrogen excretion was about 112 $\mu moles\ m^{-2} \cdot hr^{-1}$, or about 26 percent of the nitrogen increase through these tanks. Thus excretion by this taxon alone can provide a substantial nutrient source to the alga. Nutrient supply to the *Dictyosphaeria* community in the bay is probably accomplished in large part by heterotrophic oxidation of particulate organic materials.

The data from the experiment can also be used to examine the effects of light. Figure 48 demonstrates that at full sunlight the *Dictyosphaeria* biomass increased at a rate of about 0.3 percent per day. The one exception to this was the control community at Ulu-

TABLE 46

MACROBIOTA COMPOSITION OF 0.05 m^2 SUBSAMPLES REMOVED FROM THE *Dictyosphaeria cavernosa* COMMUNITIES AT THE END OF THE EXPERIMENT (Total wet weight, in grams)

LIGHT TREATMENT (% OF AMBIENT)	100	100	100	40	40	40	15	15	15
AMMONIUM LOADING ($\mu mole \cdot m^{-2} \cdot hr^{-1}$)	0	400	1200	0	400	1200	0	400	1200
Oligotrophic conditions (Ulupau)									
Plants									
Dictyosphaeria cavernosa	4,700	4,500	—	5,900	3,000	—	2,200	3,100	—
Animals									
crustaceans	210	30	—	10	6	—	5	1	—
echinoderms	0	0	—	0	2	—	1	0	—
solitary tunicates	0	0	—	0	80	—	180	0	—
polychaetes	6	0	—	0	0	—	1	0	—
Animal Biomass	220	30	—	10	90	—	190	1	—
% of Total	5	1		0.2	3		9	0.03	
Filter Feeders	0	0	—	0	80	—	180	0	—
% of Animals	0	0		0	91		96	0	
Eutrophic conditions (Coconut Island)									
Plants									
Dictyosphaeria cavernosa	8,400	10,200	7,200	4,200	6,000	7,100	1,900	2,600	1,700
Animals									
crustaceans	20	150	50	3	30	280	30	10	150
echinoderms	110	70	40	20	30	30	20	60	20
colonial tunicates	780	1,400	150	360	190	730	2,300	970	780
sponges	200	90	270	0	120	160	0	0	20
polychaetes	60	90	6	30	1	6	2	0	0
Fish	0	2	0	0	0	0	2	0	0
Animal Biomass	1,120	1,800	510	410	320	1,210	2,350	1,040	970
% of Total	12	15	7	9	6	15	55.0	29	36
Filter Feeders	980	1,490	420	360	310	890	2,300	970	800
% of Animals	84	83	82	88	84	74	98	93	82

pau, where the incoming water was low in particulate organic materials. Below full sunlight, *Dictyosphaeria* growth decreased. Our data are insufficient to construct a detailed growth curve, but the compensation intensity below which *Dictyosphaeria* showed net weight loss occurred near 150 langleys $\cdot$ day^{-1}.

These data can be used to construct a generalized model of the maximum depth of *Dictyosphaeria* net growth as a function of ambient light and light extinction coefficient. Equation 6 can be rearranged to solve for depth to which 150 langley $\cdot$ day^{-1} will penetrate (Z) as a function of ambient light (I_o) and extinction coefficient (k):

$$Z = \frac{-1}{k} \ln\left(\frac{150}{I_o}\right) \tag{8}$$

Summer and winter extreme ambient light levels are taken to be 450 and 260 langley. day^{-1}, respectively (from Figure 13), and pre- and postdiversion extinction coefficients for each sector appear in Figure 29.

Table 47 suggests that the seasonal variation of maximum *Dictyosphaeria* growth should have varied by about 2 m (between 2 and 4 m depth) in the transition zone and that in the OF sector wintertime *Dictyo-*

TABLE 47

SEASONAL AND SPATIAL VARIATION IN EXPECTED MAXIMUM DEPTH OF NET *Dictyosphaeria* GROWTH IF IT IS LIMITED TO LIGHT LEVELS ABOVE 150 LANGLEYS · DAY^{-1}

	EXTINCTION COEFFICIENT ($1 \cdot m^{-1}$)	DEPTH (meters)	
		MAXIMUM AMBIENT LIGHT (450 ly · day^{-1})	MINIMUM AMBIENT LIGHT (260 ly · day^{-1})
NW			
pre	0.30	3.7	1.8
post	0.23	4.8	2.4
CE			
pre	0.28	3.9	2.0
post	0.25	4.4	2.2
SE			
pre	0.35	3.1	1.6
post	0.29	3.8	1.9
OF			
pre	0.68	1.6	0.8
post	0.42	2.5	1.3

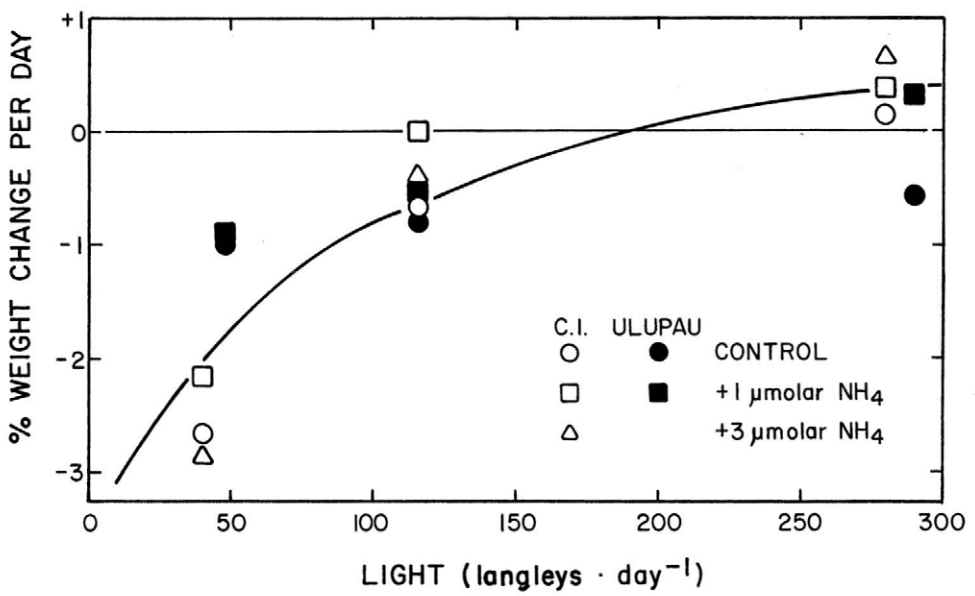


FIGURE 48. Growth rate of *Dictyosphaeria cavernosa* in response to light level and external nutrient loading.

sphaeria growth would be limited (even now) to about 1 m. It thus appears that lowered water clarity would virtually exclude *Dictyosphaeria* from the reef slope (> 1.5 m) in the vicinity of the sewer outfall.

We therefore conclude that the maximum biomass of *Dictyosphaeria cavernosa* in Kaneohe Bay was stimulated by nutrients delivered as dissolved and (perhaps more importantly) particulate materials. The high filter-feeding animal biomass associated with the *Dictyosphaeria* converted particulate organic materials to dissolved inorganic nutrients available for algal uptake. With the

reduction in particulate organic matter after diversion, the animals died and the *Dictyosphaeria* was not able to grow from its low winter biomass to the normal high summertime values. Both the depth of vertical penetration of *Dictyosphaeria* down the reef slopes and the abundance of *Dictyosphaeria* in turbid waters are also substantially restricted by light. At least up to surface ambient light levels, community growth is light-limited. Sewage nutrient loading and associated turbidity from particulate organic materials thus acted as both stimulus and inhibitor to *Dictyosphaeria* growth. Other factors (e.g., substratum, grazing, etc.) undoubtedly also affect the distribution of this alga.

LAGOON-FLOOR COMMUNITY METABOLISM: Preliminary analyses (Smith 1977) suggested that the lagoon sediments figured prominently in nutrient cycling within the bay and were thus likely to be closely linked to sewage loading and its diversion. Observations for other ecosystems (summarized by Nixon 1981) lend credence to this hypothesis. Harrison (1981) has examined the role of lagoon-floor benthic macrofauna, especially the alpheid shrimp *Alpheus mackayi*, in Kaneohe Bay. In the following section we consider that investigation in the context that lagoon-floor metabolism might have been stimulated by sewage discharge and be depressed by its diversion.

Benthic respiration and nutrient release from the sediments to the water column were measured by emplacing Plexiglas hemispheres ("domes"), 1 m in diameter, on the lagoon floor, measuring changes in water composition within the domes over approximately 24-hour periods and calculating release rates per unit area of lagoon floor. Three potential problems with this technique merit brief attention:

Water might leak between the domes and the surrounding water column. A rim around the flange of each dome penetrated 10 cm into the soft lagoon mud, and dye injections demonstrated that leakage was small in comparison with observed rates of change.

Lack of water stirring within a dome might somehow alter the measured nutrient release rates. In some high-energy environments, this effect might be significant. The lagoon floor of Kaneohe Bay is characterized by very slow water flow, and the water pumping by shrimps (unaffected by the domes) probably is a significant term in the local turbulence regime. The main effect of the domes on water motion is that they stop the vertical exchange of materials in the bottom water with the overlying water column. This effect probably mimicked a natural phenomenon, inasmuch as a near-bottom "nepheloid layer" develops during periods of low wind mixing (Figure 32).

Alteration of metabolic rates might occur in response to large changes in water composition within the domes. We have already noted that the environment within the domes mimicked a natural phenomenon. Moreover, on occasion we left domes emplaced for 3–4 days and eventually induced a variety of chemical and biological responses to this deliberately extreme treatment. In particular, oxygen release slowed; some organisms burrowed out from under the dome collars; others left their burrows and came to the sediment surface; some died. We assume these responses primarily reflected the low oxygen levels. Hourly examination of oxygen levels over emplacements of 1–2 days yielded smooth changes in oxygen concentration with no evidence of the behavioral anomalies described above.

Having considered what we believe to be the three most likely problems with this technique, we accept the measurements as an approximation of metabolic processes on the lagoon floor. Table 48 summarizes nutrient and oxygen flux measurements made on the lagoon floor in the three sectors before and after sewage diversion.

For each of these materials there were significant prediversion differences among the sectors. The differences were most conspicuous for ammonium and oxygen, with the SE/OF sector showing the highest rates of flux. Nitrate flux was minor relative to ammonium. Both before and after sewage diversion the ammonium-plus-nitrate-to-phosophate release ratio averaged about

TABLE 48

RELEASE OF INORGANIC NUTRIENTS AND OXYGEN UPTAKE OVER 24-HOUR PERIODS
($mmoles \cdot m^{-2} \cdot day^{-1}$)

SOFT-BOTTOM AREA ($10^6 m^3$)	NW 4.81			CE 7.91			SE/OF 5.98			BAY MEAN 18.70
	MEAN ± 95%	N	MEDIAN	MEAN ± 95%	N	MEDIAN	MEAN ± 95%	N	MEDIAN	
NH_4										
pre	0.61 ± 0.22	18	0.47	1.31 ± 0.40	15	1.17	1.86 ± 0.49	17	1.66	1.31
post	0.49 ± 0.09	18	0.16	1.07 ± 0.43	17	0.87	0.96 ± 0.31	15	0.88	0.89
NO_3										
pre	0.17 ± 0.08	18	0.14	0.00 ± 0.02	17	0.00	0.18 ± 0.05	17	0.17	0.10
post	0.19 ± 0.07	18	0.16	0.00 ± 0.03	17	0.00	0.22 ± 0.09	15	0.20	0.12
PO_4										
pre	0.048 ± 0.023	16	0.040	0.055 ± 0.019	17	0.050	0.110 ± 0.036	16	0.094	0.071
post	0.047 ± 0.021	18	0.051	0.016 ± 0.038	18	0.014	0.082 ± 0.033	15	0.083	0.045
Si										
pre	0.89 ± 1.65	18	1.48	3.51 ± 1.37	15	4.02	4.30 ± 0.85	17	4.73	3.09
post	2.57 ± 1.49	18	2.56	2.34 ± 2.23	18	2.57	4.40 ± 1.45	15	4.42	3.06
O_2										
pre	−11.4 ± 3.0	18	−9.7	−12.5 ± 3.9	19	−10.3	−18.3 ± 2.4	17	−18.1	−14.1
post	−10.0 ± 3.0	16	−9.5	−4.9 ± 3.0	18	−3.6	−11.9 ± 3.5	16	−11.5	−8.5

TABLE 49

COMPARISON OF SOFT-SEDIMENT NUTRIENT RELEASE RATES WITH DISSOLVED INORGANIC NUTRIENT LOADING AND THE 30-CM RESERVOIR OF THE SOUTHERN BASIN

	DISSOLVED INORGANIC LOADING (kmoles·day^{-1})	30-cm DISSOLVED NUTRIENT RESERVOIR (kmoles)	30-cm PARTICULATE NUTRIENT RESERVOIR (kmoles)	SEDIMENT NUTRIENT RELEASE (kmoles·day^{-1})
Nitrogen				
pre	11	354	150,000	12
post	3			7
Phosphorus				
pre	1.9	32	52,000	0.7
post	0.1			0.5
Silicon				
pre	17	420	? large	26
post	27			26

20 : 1 (i.e., about the ratio found in water-column particulate organic materials, Figure 23).

The release rate of ammonium and phosphate and the uptake of oxygen decreased after sewage diversion at all stations. For ammonium, the decrease was most strongly evident in the SE/OF sector. The decreased postdiversion oxygen and phosphate fluxes in the CE sector may be either a statistical artifact or a result of benthic algal growth and autotrophy on the lagoon floor. In either case, we interpret the data as showing a relationship between nutrient loading and release from the sediments.

Table 49 presents the sediment nutrient release data from the southern basin in comparison with 30-cm dissolved and particulate nutrient reservoirs and with the inorganic nutrient loading. As discussed in Sediment Composition, 30 cm is about the depth of active biological stirring (bioturbation) and thus is a reasonable first approximation of the sediment nutrient reservoir which was directly interactive with the overlying water column. Several conclusions emerge. Nutrient release was close to nutrient loading. The 30-cm sediment dissolved nutrient reservoir before sewage diversion was enough to account for less than two months' release at the prediversion rate. The fact that release during the postdiversion period in the southern basin remains higher than release elsewhere probably reflects coutinued higher particulate concentration and probably higher sedimentation there than elsewhere. There may also be a certain long-term release from the largely refractory particulate organic materials that accumulate in the sediments. Such a long-term reservoir is suggested by the elevated dissolved nitrogen and phosphorus levels below 30 cm in the sediment cores. Further monitoring and analysis would be necessary to quantify this partitioning into short-term and long-term sediment nutrient reservoirs.

Several other points emerge from this research. The presence of alpheid shrimp burrowing into the sediments and flushing water through burrows into the overlying water column raises nutrient release rates well above the rates that would be calculated from physical models of nutrient diffusion. The advection of water pumped by the shrimp thus exercises some control on the nutrient concentration of the interstitial water. In the absence of the shrimp, interstitial nutrient levels would probably increase. The sediments might become anoxic; if so, the characteristics of sediment community metabolism and biological structure would change. The behavioral responses of larger

TABLE 50

COMMUNITY NUTRIENT FLUX IN THE SOUTHERN BASIN OF KANEOHE BAY
(kmoles·day^{-1})

NUTRIENT	INORGANIC LOADING	INORGANIC EXPORT	PHYTO-PLANKTON UPTAKE	ZOO-PLANKTON RELEASE*	SHALLOW BENTHOS FLUX†	LAGOON BENTHOS FLUX	IMBALANCE
Nitrogen							
pre	+11	−2	−93	+31 to +62	+28	+12	−13 to +18
post	+2	0	−33	+22 to +45	0	+7	−2 to +21
Phosphorus							
pre	+1.9	−1.5	−5.8	+4.4	+1.7	+0.7	+1.4
post	+0.1	−0.3	−2.0	+3.3	0	+0.5	+1.6

NOTE: Each figure refers to dissolved inorganic nutrients or readily available organic nutrients.

*The uncertainty in the zooplankton nitrogen release reflects uncertainty in the fraction of the organic nutrient excretion that is urea and therefore likely to be useable.

†It is assumed that the shallow benthos net flux dropped to near 0 after sewage diversion, on the bases that both the plant and animal biomass decreased dramatically and also that normal reefs have a production-to-respiration ratio near 1. It is possible that postdiversion nitrogen fixation may now be as high as 10 kmoles·day^{-1}.

biota to anoxia in the domes were indications that the extant community is not adapted to vanishingly low dissolved oxygen levels.

Finally, Harrison (1981) demonstrates that the observed rates of oxygen and nutrient flux of the lagoon floor are not attributable to direct metabolic rates of the shrimps themselves. His calculations suggest that shrimp metabolism directly accounts for less than 10 percent of the observed nutrient fluxes and less than 20 percent of the oxygen flux.

We conclude that nutrient regeneration in the sediments and release to the water have been responsive to sewage loading and its diversion. There is an active short-lived nutrient reservoir which results from particulate material production in the ecosystem, fallout to the sediments, and oxidation there. However, the much larger and longer-lived particulate nutrient reservoirs derived from stream loading of detritus may also be significant. Metabolism on the lagoon floor is largely attributable to microorganisms, which are in turn responsive to the supply of particulate organic substrate. These organisms are also apparently responsive to the interstitial oxygen content of the sediments. Larger organisms, while responsible for only a small fraction of the nutrient regeneration by their direct metabolic activity, flushed the nutrients more rapidly than diffusion models would imply and probably control the biotic and chemical composition of the sediments thereby.

TOTAL COMMUNITY NUTRIENT CYCLING IN THE SOUTHERN BASIN: Table 50 summarizes the various nutrient cycling calculations that have been presented in this section and compares these internal cycles with the net loading minus export of dissolved nutrients (from Nutrient Cycling in the Southern Basin). The material considered here consists of dissolved inorganic nutrients. Since much of the nitrogen excreted by zooplankton may be urea, and since urea is readily available to phytoplankton, the possible urea excretion has been included. Figures for urea loading and export are unknown but likely to be small.

The internal nutrient cycles are large relative to the nutrient loading and loss rates. As presented, the phytoplankton uptake and the zooplankton excretion dominate the cycling. In fact, uncertainties in the cycling, primarily in the magnitude and composition of zooplankton excretion, and secondarily in the flux estimates of the shallow benthos community, exceed the input minus output terms.

The importance of this tabulation, besides emphasizing remaining gaps in our knowledge of Kaneohe Bay, is the observation that at any instant the system is largely processing

TABLE 51

SUMMARY OF DIVERSION AND SPATIAL RESPONSES OF VARIABLES IN FIGURE 49

NUMBER	GROUP	VARIABLE	DIVERSION RESPONSE (PERCENT)	GRADIENT RESPONSE (OF : SE)	SOURCE
1	1	Dissolved inorganic nitrogen	37	1.4	Table 8
2	2	Dissolved inorganic phosphorus	70	1.8	Table 9
3	1	Particulate organic carbon	36	1.3	Table 11
4	1	Phytoplankton biomass	37	2.3	Table 11
5	1	Phytoplankton growth rate	36	1.0	Table 35
6	1	Macroplankton dry weight	35	2.7	Table 22
7	1	Microplankton ash-free dry weight	35	1.9	Table 22
8	2	Hard bottom algal biomass	62	0.2	Table 29
9	2	Hard bottom cryptofaunal biomass	76	2.5	Table 34
10	2	Lagoon floor biomass	83	0.4	Table 34
11	1	Lagoon floor nitrogen release	42	1.3	Table 44
12	~1	Extinction coefficient	25	1.8	Table 12
13	3	Detritus	8	1.2	Table 21
Qualitative Variables: Community Structure					*Biotic composition*
14	3	Zooplankton	slight	moderate	zooplankton
15	3	Benthic algae	slight to moderate	slight	benthic algae
16	3	Benthic macrofauna	slight or none	moderate	benthic community and fishes
17	3	Fish	none ?	large	benthic community and fishes

NOTE: For quantitative variables the numbers given are percent decrease in the southern basin (volume-weighted means of SE and OF) and the ratio of postdiversion values at OF to transition zone (volume- or area-weighted means of NW and CE). For community structures (qualitative variables) the relative sizes of the responses are indicated.

internally cycled nutrients rather than new nutrients. This general observation is consistent with previous information about Kaneohe Bay (Caperon 1975; Harvey and Caperon 1976) and with information about other coastal marine ecosystems (e.g., Davies 1975; Kremer and Nixon 1978; Nixon et al. 1980; Rowe, Clifford, and Smith 1977; Rowe et al. 1975).

Summary

In our discussion of the dynamics of material processing in the bay, with emphasis on the southern basin, we have demonstrated that nitrogen is the limiting nutrient, and that recycling supports far more planktonic productivity than does direct nutrient input. The effect of nutrient input is to control, in concert with bay flushing, the biomass of the plankton. Productivity is controlled by recycling and by light.

Benthic community metabolism seems to be controlled primarily by particulate loading. The reefs in the southern basin were more heterotrophic than those to the north, apparently because of the high supply rate of particulates and their obstruction of light. The biomass of the alga *Dictyosphaeria cavernosa* was apparently also supported by particulate matter because of the dense epizoic communities and attendant nutrient recycling. We also showed that lagoon floor metabolism provided a major source of recycled nutrients, which decreased substantially following sewage diversion.

Our models of total nitrogen and phosphorus and inorganic nitrogen and phosphorus fluxes and concentrations (Figure 43 and Table 50) point to remaining gaps in our knowledge of system dynamics. The degree of imbalance in the mass balance model is not well explained, and suggests a need for more detailed study of material cycling in the bay.

SUMMARY AND CONCLUSIONS

The Kaneohe Bay experiment addressed the utility of the hypothesis that:

Domestic sewage discharge into ecosystems exerts an influence by modifying biomass and foodweb characteristics of those systems. Hence, ecosystem responses to sewage and its diversion can be ascertained from a comprehensive description of nutrient addition to the system, storage and cycling within the system, and flushing from the system.

The delivery of sewage-derived inorganic plant nutrients and the termination of that delivery represented the experiment in nutritional perturbation. As is generally the case for marine ecosystems receiving domestic sewage (see Ryther and Dunstan 1971), dissolved nitrogen was the nutrient present in shortest supply.

Ecosystem Response

The responses of numerous variables measured during this study are summarized in Figure 49 and Table 51. Specifically, there were two classes of variables: those to which numbers could be assigned (biomasses or rates) and those which had to be evaluated subjectively (community composition). For the numerical variables, we computed the diversion response as the percent decrease in each value for the southern basin, volume averaged for the water column variables. We also computed a spatial gradient as the ratio of the postdiversion value at station OF and in the transition zone, calculated from the NW and CE values and weighted by area or volume as appropriate.

Figure 49 shows that the responses fall into three groups: one with moderate diversion and spatial responses (group 1); one with a large diversion response but with a wide range of spatial responses (group 2); and one with little response to sewage diversion and a slight-to-large spatial gradient (group 3).

The variables in group 1 include all of the measures of water-column biomass plus water-column dissolved inorganic nitrogen and benthic nutrient flux. One consequence of nitrogen being the most limiting nutrient was that dissolved inorganic nitrogen showed

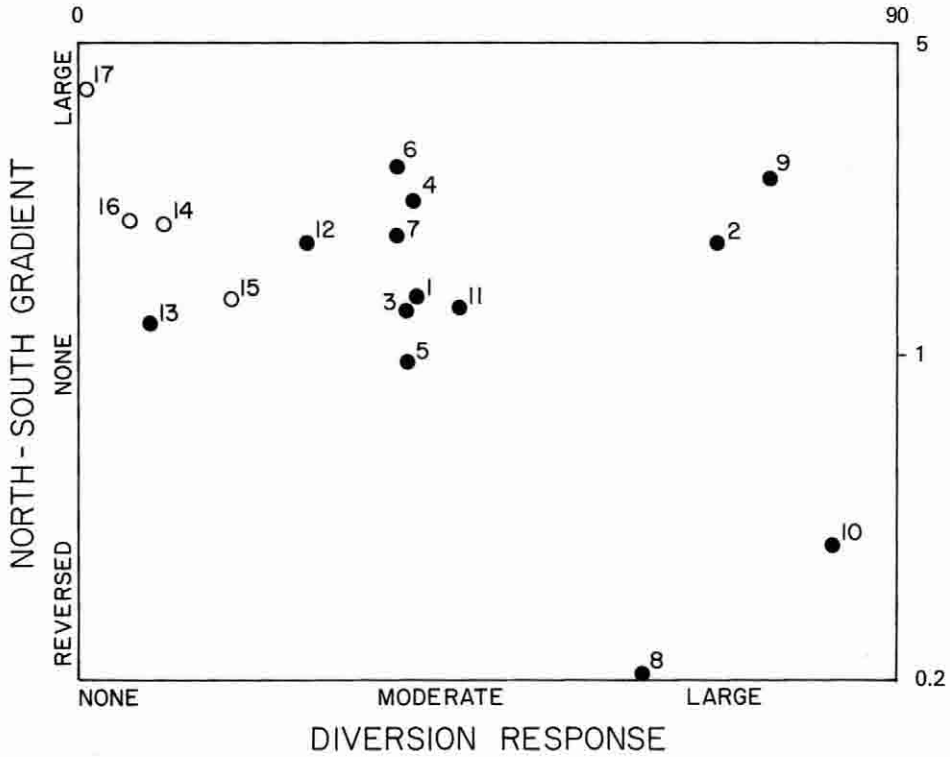


FIGURE 49. Summary of responses of selected variables to sewage diversion and to the north-south spatial gradient. Solid circles represent variables for which the responses can be quantified (scales at top and right), while open circles represent qualitative variables. See Table 51 for identification of the variables, the values, and sources of information.

no greater diversion or spatial response than measures of particulate matter. The signature of the sewage was equally apparent in dissolved inorganic nitrogen, particulate carbon and nitrogen, and chlorophyll. In contrast, dissolved inorganic phosphorus showed a large sewage response and a much larger spatial gradient than did nitrogen.

Although the proportional change in dissolved inorganic nitrogen was similar to those of chlorophyll and other biomass measures, the magnitude of that change was smaller (see Ecosystem Composition: Nitrogen). The dissolved inorganic nitrogen concentration decreased to only slightly above the background oceanic value, while the particulate levels remained several times higher than oceanic levels. Most of the nutrient input to the bay became incorporated in particulate matter.

The small magnitude of the decrease in dissolved inorganic nitrogen suggests that measurement of the limiting nutrient concentration is a poor indicator of eutrophication. A more useful indicator would be chlorophyll or some other particulate material, since most of the nitrogen is rapidly incorporated into the particulate fraction. The concentration of dissolved inorganic nitrogen is more an indicator of rapid recycling than input, although recycling is of course positively related to total system biomass.

An examination of mean prediversion concentrations of dissolved inorganic nitrogen and phytoplankton and zooplankton biomass yields some insight into the function of this system (Ecosystem Composition). The ratios of each mean value to the values at station NW show that the zone of influence of nutrient concentration was largely con-

fined to the outfall area; the zone for phytoplankton chlorophyll extended throughout the southern basin; and that for zooplankton could be seen also at station CE. The pattern of nutrient concentration and phytoplankton and zooplankton biomass can be regarded as crudely analogous to a chemostat with nutrient input in the south and aging, mixing, and washout to the north. The pattern reflects the increasing turnover times from dissolved nutrient to phytoplankton and zooplankton.

Dissolved organic nitrogen (DON), not shown in Figure 49, actually increased by 15 percent in the southern basin (Ecosystem Composition: Nitrogen). Although part of the increase could be attributed to a small but significant annual cycle, the increase itself was significant. The small spatial gradient and reversed diversion response suggest that DON is largely inactive in the water-column nitrogen cycle. The increase in DON may have resulted from the increased rainfall after sewage diversion, and we assume that it is almost entirely refractory.

The variables in group 2 (Table 51), which showed a large sewage response, included dissolved inorganic phosphorus and several benthic biomass measures. As discussed above, the diversion response of phosphate was large because before diversion the system was far from phosphorus limitation.

The large response of the benthic biomass variables reflects enhanced prediversion delivery of particulate matter to the benthos. The location of the southern benthic station under the outfall plume contributed to the prediversion particle flux. This elevated flux was reflected in the enhanced biomass and to some extent in the elevated nutrient regeneration rate (Table 48). Spatial gradients of the benthic biomass variables were equivocal. Benthic algae were most abundant at some distance from the outfall. Low light caused by the water-column particulate load (see *Dictyosphaeria cavernosa* Metabolism) and perhaps lack of substratum due to substratum utilization by other benthic organisms apparently limited algal buildup near the outfall; higher light combined with nutrient release by benthic animals favored algal growth at an intermediate distance from the outfall.

Benthic plants and animals both responded to sewage diversion by decreasing in biomass. The postdiversion period of investigation was insufficient to ascertain the extent of benthic biomass and compositional response to diversion. The timespan of initial response was rapid, but postdiversion conditions of the benthos did not match presewage conditions by the end of this investigation. In part, this result can be explained by the destruction or burial of hard substratum by both sewage-mediated biological activity and siltation from heavy runoff. The results of these processes can be reversed only slowly if at all. The long turnover times of conspicuous reef organisms such as corals also lengthen the time scale for succession of the benthos. As this is written (mid 1981) partial recovery of coral communities has become evident.

Although it might be hypothesized that the decline in benthic biomass added nitrogen to support the planktonic system, we have no evidence to show that to be the case. On the contrary, the initial benthic response was rapid and not accompanied by a gradual decline in water-column values. Thus it is likely that the biomass lost by the benthos was either buried or washed quickly from the system.

The group 3 variables (Table 51) included the detrital standing crop and the qualitative variables of community structure. These changed little with sewage diversion. The small change in detritus reflects the relative unimportance of nutrient input for the maintenance of a detrital pool. This appears to be a largely refractory material derived from some combination of runoff and resuspension of sediments.

The community structure variables showed various spatial gradients, for the most part reflecting changes in habitat. The lack of major compositional shifts during sewage diversion may indicate that the sewage was a minor stress on these components; alternatively, except for the zooplankton, it may indicate that the habitat has not had time to revert to a presewage condition.

Guidelines for Similar Research

One of our purposes in attempting this study was to arrive at the most efficient possible approach to the ecosystem experiment. Our successes and failures in this endeavor could provide a starting point for similar research.

A major strength of this study was its integration of various aspects of whole-ecosystem research, which enabled us to learn more about the system than would have been possible with an assortment of unconnected projects.

Another strength was the use of a chemostat-like model as a conceptual framework, at least for the water-column investigations. We found such a conceptual model to be of great assistance in integrating the efforts of the various research groups and in assembling this report.

Some weaknesses of course became apparent under the critical focus of hindsight. We did not recognize until relatively late the importance of meteorological events. Hence, we missed an opportunity to make all of our measurements synoptic, which would have enabled us to use more powerful statistical techniques in our data analysis.

In any study such as this there arise questions about the level of effort to be expended in obtaining various pieces of information. In this study these conflicts were resolved largely by the degree of difficulty involved in some of the measurements. For this reason our phytoplankton sampling effort focused on biomass and metabolism and virtually ignored species composition; the zooplankton effort was aimed more at taxonomic detail than at metabolism. The leader of every such project must personally decide how this conflict is to be resolved, but it must be done if the entire effort is to fit into a conceptual model of how the system is supposed to work.

In that connection, we might have been better advised to switch efforts from, say, taxonomic detail about the zooplankton or benthos to concentration on metabolic aspects. In hindsight, better information on zooplankton excretion or benthic nitrogen fixation might have proved useful. At the time the decisions were being made, of course, we did not know what the system would do or how best to observe the changes that would occur. The only way to handle this dilemma is to decide on a course of action at the outset, alter it if necessary early in the program, and then maintain the chosen level of effort to the end.

The advantage that accrues from a decisive, if not entirely ideal, approach is that the resulting data set might be long enough to provide some statistical meaning to observed changes. It is apparent from the results of this and other studies that long-term data collections are necessary to overcome the extreme and irregular variability of even subtropical environments. Our study might have benefited from an additional two years of data collection before and after sewage diversion, particularly in view of the change in rainfall that occurred after the second year.

We found a mass-balance model to be the most useful framework for the analysis of system responses to perturbation. A similar approach has been used elsewhere, and might prove generally useful in coastal ecosystem studies. The study of Lake Washington response to sewage diversion (Edmondson 1977; Edmondson and Lehman 1981) incorporated a mass-balance model differing in two major respects from ours. First, the Lake Washington study treated nutrient fallout to the benthos as output from a plankton-dominated system. Benthic metabolism and nutrient cycling are prominent in Kaneohe Bay and are therefore accorded major consideration. Second, Lake Washington is a closed system in which outputs can be measured, and recycling and sequestering of nutrients within the lake can be calculated by difference. Kaneohe Bay and other coastal ecosystems exchange material with the ocean through tidal advection and turbulent diffusion, making the calculation of nutrient output and retention orders of magnitude more difficult.

In 1975 an international symposium on the recovery of damaged ecosystems was held in Blacksburg, Virginia. Cairns,

Dickson, and Herricks (1977) summarized the papers and the subsequent discussion with the following recommendations:

1. A real need exists for a comprehensive effort to synthesize the existing information on the restoration and recovery of ecosystems after damage.
2. A series of well-planned and comprehensive baseline studies of representative ecosystems should be undertaken.
3. Future studies on the recovery process should include measurements of the functional characteristics as well as structural characteristics of the ecosystem.

We have used the Kaneohe Bay experiment to realize each of the above recommendations on a single ecosystem. We believe that our research has led to generalities about the responses of marine ecosystems to perturbation (especially nutritional perturbation); we believe that a comprehensive total-ecosystem analysis of nutrient fluxes leads to conclusions not easily derived from numerous single-component studies; and we believe that the use of major, planned technological events as total-ecosystem experiments has a value that has not in the past been sufficiently appreciated.

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LITERATURE CITED

AL-HUSSAINI, A. H. 1947. The feeding habits and the morphology of the alimentary tract of some teleosts living in the neighborhood of the Marine Biological Station, Ghardaqa, Red Sea. Publ. Mar. Biol. Stn. Ghardaqa. 5:1–61.

ARMSTRONG, F. A. J., P. M. WILLIAMS, and J. D. H. STRICKLAND. 1966. Photo-oxidation of organic matter in sea water by ultra-violet radiation, analytical and other applications. Nature 211:481–483.

ATKINSON, M. 1981. Phosphate metabolism of coral reef flats. Ph.D. Thesis. University of Hawaii, Honolulu. 70 pp.

ATKINSON, M., and S. V. SMITH. (submitted) Carbon-nutrient ratios of benthic marine plants. Submitted to Mar. Ecol. Progr. Ser.

BANNER, A. H. 1968. A fresh water "kill" on the coral reefs of Hawaii. University of Hawaii, Hawaii Inst. Mar. Biol. Tech. Rep. 15. 29 pp.

———. 1974. Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. Pages 685–702 *in* Proc. 2d Internat. Symp. Coral Reefs. Vol. 2. Great Barrier Reef Committee, Brisbane.

BANNER, A. H., and J. H. BAILEY. 1970. The effects of urban pollution upon a coral reef system: a preliminary report. University of Hawaii, Hawaii Inst. Mar. Biol. Tech. Rep. 25. 66 pp.

BANNISTER, T. T. 1974. A general theory of steady state phytoplankton growth in a nutrient saturated mixed layer. Limnol. Oceanogr. 19:13–30.

BARTHOLOMEW, E. F. 1973. The production of microcopepods in Kaneohe Bay, Oahu, Hawaii. M.S. Thesis. University of Hawaii, Honolulu. 43 pp.

BARTRAM, P. D. 1976. A performance standard for erosion control. University of Hawaii, Hawaii Environmental Simulation Lab. Tech. Rep. 3. 36 pp. + appendices.

BATHEN, K. H. 1968. A descriptive study of the physical oceanography of Kaneohe Bay, Oahu, Hawaii. University of Hawaii, Hawaii Inst. Mar. Biol. Tech. Rep. 14. 353 pp.

BOSCH, H. F. 1967. Growth rate of *Fungia scutaria* in Kaneohe Bay, Oahu. M.S. Thesis. University of Hawaii, Honolulu. 38 pp.

BROCK, R. E., and J. H. BROCK. 1977. A method for quantitatively assessing the infaunal community in coral rock. Limnol. Oceanogr. 22:948–951.

BROCK, R. E., C. LEWIS, and R. C. WASS. 1979. Stability and structure of a fish community on a coral patch reef in Hawaii. Mar. Biol. 54:281–292.

BROCK, R. E., and S. V. SMITH. (submitted) Response of coral reef cryptofaunal communities to food and space. Submitted to Coral Reefs.

BROCK, V. E. 1954. A preliminary report on a method of estimating reef fish populations. J. Wildl. Manage. 18:297–308.

CAIRNS, J. JR., K. L. DICKSON, and E. E. HERRICKS. 1977. The recovery and restoration of damaged ecosystems, a challenge for actions: symposium analysis. Pages 522–525 *in* J. Cairns, Jr., K. C. Dickson, and E. E. Herricks, eds. Recovery and restoration of damaged ecosystems. University of Virginia Press, Charlottesville.

CAPERON, J. 1975. A trophic level ecosystem model analysis of the plankton community in a shallow-water subtropical estuarine embayment. Pages 691–709 *in* L. E. Cronin, ed. Estuarine research. Vol. 1. Chemistry, biology and the estuarine system. Academic Press, New York.

CAPERON, J., S. A. CATTELL, and G. KRASNICK. 1971. Phytoplankton kinetics in a subtropical estuary: eutrophication. Limnol. Oceanogr. 16:599–607.

CAPERON, J., W. A. HARVEY, and F. A. STEINHILPER. 1976. Particulate organic carbon, nitrogen, and chlorophyll as measures of phytoplankton and detritus standing crops in Kaneohe Bay, Oahu, Hawaiian Islands. Pac. Sci. 30:317–327.

CAPERON, J., D. SCHELL, J. HIROTA, and E. LAWS. 1979. Ammonium excretion rates in Kaneohe Bay, Hawaii, measured by a ^{15}N isotope dilution technique. Mar. Biol. 54:33–40.

CHAN, A. T. 1978. Comparative physiological study of marine diatoms and dinoflagellates in relation to irradiance and cell size. I. Growth under continuous light. J. Phycol. 14:396–402.

CLUTTER, R. I. 1973. Plankton ecology. University of Hawaii, Water Resources Research Center Tech. Rep. 31:185–213.

CORNER, E. D. S., and A. G. DAVIES. 1971. Plankton as a factor in the nitrogen and phosphorus cycles in the sea. Adv. Mar. Biol. 9:101–204.

DAMES and MOORE. 1977. Kaneohe Bay urban water resources study. Kaneohe Bay computer modeling, Kaneohe, Hawaii, for U.S. Army Engineer District, Honolulu, Oahu. 133 pp. + supplement.

DAUER, D. M., and W. G. CONNER. 1980. Effects of moderate sewage input on benthic polychaete populations. Est. and Coastal Mar. Sci. 10:335–346.

DAVIES, J. M. 1975. Energy flow through the benthos in a Scottish sea loch. Mar. Biol. 31:353–362.

DEPARTMENT OF PLANNING AND ECONOMIC DEVELOPMENT (DPED). 1977. The State of Hawaii Data Book. Honolulu. 339 pp.

DEVANEY, D. M., M. KELLY, P. J. LEE, and L. S. MOTTELER. 1976. Kaneohe: a history of change (1778–1950). Bernice P. Bishop Museum, Honolulu. 271 pp.

DOTY, M. S. 1956. Current status of the carbon-fourteen method of assaying productivity in the ocean. Annual Report, Contract AT (04-3)-15, U.S. Atomic Energy Commission. Honolulu.

DOTY, M. S., and L. R. A. CAPURRO. 1961.

Productivity measurements in the world ocean. Pt. I. IGY Oceanogr. Rep. 4. Texas A & M, College Station. 298 pp.

DUGAN, G. L. 1977. Water quality of normal and storm-induced surface water runoff: Kaneohe Bay watershed Oahu, Hawaii, February 1974 to March 1975. University of Hawaii, Water Resources Research Center Tech. Rep. 106. 74 pp.

EDMONDSON, C. H., and W. M. INGRAM. 1939. Fouling organisms in Hawaii. Bernice P. Bishop Museum, Occ. Pap. 14:251–300.

EDMONDSON, W. T. 1977. Trophic equilibrium in Lake Washington. U.S. Environmental Protection Agency, Corvallis, Oregon. Rep. EPA 600/3-77-087.

EDMONDSON, W. T., and J. T. LEHMAN. 1981. The effect of changes in the nutrient income on the condition of Lake Washington. Limnol. Oceanogr. 26:1–29.

ELKINS, J. W. 1978. Aquatic sources and sinks for nitrous oxide. Ph.D. Thesis. Harvard University, Cambridge, Mass. 5 separately numbered chapters.

EPPLEY, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. 70:1063–1085.

EPPLEY, R. W., E. H. RENGER, E. L. VENRICK, and M. M. MULLIN. 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the north Pacific Ocean. Limnol. Oceanogr. 18: 534–551.

GERHART, D. Z., and G. E. LIKENS. 1975. Enrichment experiments for determining nutrient limitation: four methods compared. Limnol. Oceanogr. 20:649–653.

GOLDMAN, B., and F. H. TALBOT. 1975. Aspects of the ecology of coral reef fishes. Pages 125–154 *in* O. A. Jones and R. Endean, eds. Biology and geology of coral reefs. Vol. 3, Biology 2. Academic Press, New York.

GORDON, J. A., and P. HELFRICH. 1970. An annotated bibliography of Kaneohe Bay. University of Hawaii, Hawaii Inst. Mar. Biol. Tech. Rep. 20. 260 pp.

GRAY, B., and L. S. LAU. 1973. Alternative methods for sewage disposal. University of Hawaii, Water Resources Research Center Tech. Rep. 37:343–412.

HANSON, R. B., and K. R. GUNDERSEN. 1976. Bacterial nitrogen fixation in a polluted coral reef flat ecosystem, Kaneohe Bay, Oahu, Hawaiian Islands. Pac. Sci. 30: 385–393.

HARRISON, J. T. 1981. The influence of *Alpheus mackayi* on ecosystem dynamics in Kaneohe Bay. Ph.D. Thesis. University of Hawaii, Honolulu. 112 pp.

HARVEY, W. A., and J. CAPERON. 1976. The rate of utilization of urea, ammonium, and nitrate by natural populations of marine phytoplankton in a eutrophic environment. Pac. Sci. 30:329–340.

HEIN, F. J., and M. J. RISK. 1975. Bioerosion of coral heads: inner patch reefs, Florida reef tract. Bull. Mar. Sci. 25:133–138.

HENDERSON, R. S., S. V. SMITH, and E. C. EVANS III. 1976. Flow-through microcosms for simulation of marine ecosystems: development and intercalibration of open coast and bay facilities. Naval Undersea Center, Tech. Rep. NUCTP519. 80 pp.

HIATT, R. W., and D. W. STRASBURG. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65–127.

HIROTA, J., and J. P. SZYPER. 1975. Separation of total particulate carbon into inorganic and organic components. Limnol. Oceanogr. 20:896–900.

———. 1976. Standing stocks of zooplankton size-classes and trophic levels in Kaneohe Bay, Oahu, Hawaiian Islands. Pac. Sci. 30:341–361.

HOLLETT, K. J. 1977. Shoaling of Kaneohe Bay, Oahu, Hawaii, in the period 1927 to 1976, based on bathymetric, sedimentological, and geographical studies. M.S. Thesis. University of Hawaii, Honolulu. 145 pp.

HOLM-HANSEN, O. 1970. ATP levels in algal cells as influenced by environmental conditions. Plant and Cell Physiol. 11:689–700.

HOLM-HANSEN, O., and C. R. BOOTH. 1966. The measurement of ATP in the oceans and its ecological significance. Limnol. Oceanogr. 11:510–519.

HUNTER, B. L. 1978. ATP and chlorophyll *a* as estimators of phytoplankton metabolic activity and carbon biomass. M.S. Thesis.

University of Hawaii, Honolulu. 130 pp.

INGRAM, W. M. 1937. Fouling organisms in Kaneohe Bay and Pearl Harbor, Oahu. M.S. Thesis. University of Hawaii, Honolulu. 145 pp.

IVERSON, R. L., H. F. BITTAKER, and V. B. MEYERS. 1976. Loss of radiocarbon in direct use of aquasol for liquid scintillation counting of solutions containing ^{14}C-$NaHCO_3$. Limnol. Oceanogr. 21: 756–758.

JACOBS, W. C. 1942. On the energy exchange between sea and atmosphere. Jour. Mar. Res. 5:37–60.

JEFFREY, S. W. 1974. Profiles of photosynthetic pigments in the ocean using thin-layer chromatography. Mar. Biol. 26: 101–110.

JEFFREY, S. W., and G. F. HUMPHREY. 1975. New spectrophotometric equation for determining chlorophylls a, b, c_1, and c_2 in higher plants, algae, and natural phytoplankton. Biochem. Physiol. Pflanzen 167: 191–194.

JOHANNES, R. E. 1964. Phosphorus excretion and body size in marine animals: microzooplankton and nutrient regeneration. Sci. 146:923–924.

———. 1980. The ecological significance of the submarine discharge of groundwater. Mar. Ecol. Prog. Ser. 3:365–373.

JOHANNES, R. E., and the PROJECT SYMBIOS TEAM. 1972. The metabolism of some coral reef communities. BioScience 22: 541–543.

KARL, D. M. 1978. Occurrence and ecological significance of GTP in the ocean and in microbial cells. Appl. and Env. Microbiol. 36:349–355.

KARL, D. M., and P. A. LA ROCK. 1975. Adenosine triphosphate measurements in soil and marine sediments. J. Fish. Res. Bd. Can. 32:599–607.

KIEFER, D. A., and R. W. AUSTIN. 1974. The effect of varying phytoplankton concentration on submarine light transmission in the Gulf of California. Limnol. Oceanogr. 19:55–64.

KIMMERER, W. J. 1980. Plankton patchiness and ecosystem stability. Ph.D. Thesis. University of Hawaii, Honolulu. 177 pp.

KIMMERER, W. J., T. W. WALSH, and J. HIROTA. 1981. The effects of sewage discharge into a wind-induced plume front. Pages 531–548 *in* B. Neilson and L. E. Cronin, eds. Symp. nutrient enrichment in estuaries. Humana Press, Clifton, N.J.

KINSEY, D. W. 1978. Productivity and calcification estimates using slack-water periods and field enclosures. Pages 439–468 *in* D. R. Stoddart and R. E. Johannes, eds. Coral reefs: research methods. UNESCO Monographs on Oceanographic Methodology 5. Paris.

———. 1979. Carbon turnover and accumulation by coral reefs. Ph.D. Thesis. University of Hawaii, Honolulu. 284 pp.

KINSEY, D. W., and A. DOMM. 1974. Effects of fertilization on a coral reef environment. Pages 49–66 *in* Proc. 2d Internat. Coral Reef Symp. Vol. 1. Great Barrier Reef Committee, Brisbane.

KRASNICK, G. J. 1973. Temporal and spatial variations in phytoplankton productivity and related factors in the surface waters of Kaneohe Bay, Oahu, Hawaii. M.S. Thesis. University of Hawaii, Honolulu. 91 pp.

KREMER, J. N., and S. W. NIXON. 1978. A coastal marine ecosystem. Ecological Studies, Vol. 24. Springer-Verlag, Berlin-Heidelberg. 217 pp.

LAMBERSON, P. 1974. The effects of light on primary productivity in south Kaneohe Bay. M.S. Thesis. University of Hawaii, Honolulu. 41 pp.

LAU, L. S., R. H. F. YOUNG, S. K. KONNO, R. J. OLDNALL, and H. H. LEE. 1976. Wet-weather water quality monitoring, Kaneohe Bay, Oahu, Hawaii. University of Hawaii, Water Resource Research Center Tech. Rep. 100. 121 pp.

LAWS, E. A. 1980. Effects of waste-water discharges on phytoplankton communities. Pages 13–40 *in* University of Hawaii, Sea Grant Cooperative Report UNIHI-SEAGRANT-CR-80-1.

LAWS, E. A., and T. T. BANNISTER. 1980. Nutrient- and light-limited growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the ocean. Limnol. Oceanogr. 25:457–473.

Laws, E. A., and D. G. Redalje. 1979. Effect of sewage enrichment on the phytoplankton population of a subtropical estuary. Pac. Sci. 33:129–144.

MacKaye, A. L. 1916. Where coral blossoms bloom. Mid-Pacific Mag. 11:117–121.

MacKenzie, F. T., B. L. Ristvet, D. C. Thorstenson, A. Lerman, and R. H. Leeper. 1981. Reverse weathering and chemical mass balance in a coastal environment. Pages 152–187 *in* J. M. Martin, J. D. Burton, and D. Eisma. River inputs to ocean systems. UNESCO, Switzerland.

Maragos, J. E. 1972. A study of the ecology of Hawaiian reef corals. Ph.D. Thesis. University of Hawaii, Honolulu. 290 pp.

McCarthy, J. J. 1972. The uptake of urea by natural populations of marine phytoplankton. Limnol. Oceanogr. 17:738–748.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphates in natural waters. Anal. Chim. Acta 27:31–26.

Nelson, P. R., and W. T. Edmondson. 1955. Limnological effects of fertilizing Bare Lake, Alaska. Fish. Bull. 102:414–436.

Niemeyer, G. 1978. Numerical methods for the simulation of hydrodynamic and ecological processes. University of Hawaii, Hawaii Inst. Geophys. Rep. 78–1. 127 pp.

Nixon, S. W. 1981. Remineralization and nutrient cycling in coastal marine ecosystems. Pages 111–138 *in* B. Neilson and L. E. Cronin, eds. Symp. Nutrient Enrichment in Estuaries. Humana Press, Clifton, N.J.

Nixon, S. W., J. R. Kelly, B. N. Furnas, C. A. Oviatt, and S. S. Hale. 1980. Phosphorus regeneration and the metabolism of coastal marine bottom communities. Pages 219–242 *in* K. R. Tenore and B. C. Coull, eds. Marine benthic dynamics. University of South Carolina Press, Columbia.

Otte, G., and C. D. Levings. 1975. Distribution of macroinvertebrate communities on a mud flat influenced by sewage, Fraser River Estuary, British Columbia. Env. Canada, Fish. and Marine Serv. Tech. Rep. 476. 63 pp.

Perry, M. J. 1972. Alkaline phosphatase activity in subtropical central north Pacific waters using a sensitive fluorometric method. Mar. Biol. 15:113–119.

Peterson, W. T. 1975. Distribution, abundance, and biomass of the macrozooplankton of Kaneohe Bay, Oahu, Hawaii 1966–1971. University of Hawaii, Hawaii Inst. Mar. Biol. Tech. Rep. 31. 122 pp.

Pilson, M. E. Q., and S. B. Betzer. 1973. Phosphorus flux across a coral reef. Ecol. 54:581–588.

Piyakarnchana, T. 1965. The plankton community in the southern part of Kaneohe Bay, Oahu, with the special emphasis on the distribution, breeding season, and population fluctuation of *Sagitta enflata* Grassi. Ph.D. Thesis. University of Hawaii, Honolulu. 193 pp.

Poole, H. H., and W. R. G. Atkins. 1929. Photo-electric measurements of submarine illumination throughout the year. J. Mar. Biol. Assoc. U. K. 16:297–324.

Poore, G. C., and J. D. Kudenov. 1978*a*. Benthos of the Port of Melbourne: the Yarra River and Hobson's Bay, Victoria. Aust. J. Mar. Freshwater Res. 29: 141–155.

———. 1978*b*. Benthos around an outfall of the Werribee sewage-treatment farm, Port Philip Bay, Victoria. Aust. J. Mar. Freshwater Res. 29:157–167.

Randall, J. E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Carib. J. Sci. 3: 31–47.

———. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. 5:665–847.

Redfield, A. C., B. H. Ketchum, and F. A. Richards. 1963. The influence of organisms on the composition of sea water. Pages 26–77 *in* M. N. Hill, ed. The sea. Vol. 2. Wiley, New York.

Ricker, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Bd. Can. 30:409–434.

Ristvet, B. L. 1978. Reverse weathering reactions within recent nearshore sediments, Kaneohe Bay, Oahu. Defense Nuclear Agency, Subtask L48AAXYX994, Work Unit 04, Project EXPOE. 314 pp.

ROWE, G. T., C. H. CLIFFORD, K. L. SMITH, and P. L. HAMILTON. 1975. Benthic nutrient regeneration and its coupling to primary productivity in coastal waters. Nature 255:215–217.

ROWE, G. T., C. H. CLIFFORD, and K. L. SMITH. 1977. Nutrient regeneration in sediments off Cap Blanc, Spanish Sahara. Deep-Sea Res. 24:57–63.

ROY, K. J. 1970. Change in bathymetric configuration, Kaneohe Bay, Oahu, 1882–1969. University of Hawaii, Hawaii Inst. Geophys. Rep. 70–15. 26 pp.

RUMMEL, R. 1967. Understanding factor analysis. J. Conflict Resolution 11: 444–480.

RUNCHAL, A. K. 1978. Mathematical modeling study of a large water body. Coastal Zone '78, Proc. Symp. Tech. Env., socioeconomic, regulatory aspects of coastal zone mgmt. ASCE/San Francisco, pp. 1897–1916.

RYTHER, J. H., and W. M. DUNSTAN. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Sci. 171:1008–1013.

SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. Sci. 195: 260–262.

———. 1974. Eutrophication and recovery in experimental lakes: implications for lake management. Sci. 184:897–899.

SECKEL, G. R., and M. Y. Y. YONG. 1977. Koko Head, Oahu, sea-surface temperatures and salinities, 1956–1973, and Christmas Island sea-surface temperatures, 1954–1973. Fish. Bull. 75:767–787.

SKIRROW, G. 1975. The dissolved gases—carbon dioxide. Pages 1–192 *in* J. P. Riley and G. Skirrow, eds. Chemical oceanography 2. Academic Press, London.

SMITH, S. V. 1974. Coral reef carbon dioxide flux. Pages 77–85 *in* Proc. 2d. Internat. Coral Reef Symp. Vol. 1. Great Barrier Reef Committee, Brisbane.

———. 1977. Kaneohe Bay: a preliminary report on the responses of a coral reef/estuary ecosystem to relaxation of sewage stress. Pages 577–583 *in* Proc. 3d Internat. Coral Reef Symp., Vol. 2. University of Miami, Miami.

SMITH, S. V., K. E. CHAVE, and D. T. O. KAM. 1973. Atlas of Kaneohe Bay: a reef ecosystem under stress. University of Hawaii, Sea Grant Pub. TR-72-01. 128 pp.

SMITH, S. V., and P. L. JOKIEL. 1978. Water composition and biogeochemical gradients in the Canton Atoll lagoon. Atoll Res. Bull. 221:15–53.

SMITH, S. V., P. L. JOKIEL, G. S. KEY, and E. B. GUINTHER. 1979. Metabolic responses of shallow tropical benthic microcosm communities to perturbation. U.S. Environmental Protection Agency, EPA-600/3-79-061. 57 pp.

SMITH, S. V., and D. W. KINSEY. 1978. Calcification and organic carbon metabolism as indicated by carbon dioxide. Pages 469–484 *in* D. R. Stoddart and R. E. Johannes, eds. Coral reefs: research methods. UNESCO Monographs on Oceanographic Methodology 5, Paris.

SOEGIARTO, A. 1973. Benthic algae of the bay. Pages 67–90 *in* S. V. Smith, K. E. Chave, and D. T. O. Kam. Atlas of Kaneohe Bay. University of Hawaii, Sea Grant Publ. TR-72-01.

SOKAL, R. R., and F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 pp.

SOURNIA, A. 1977. Analyse et bilan de la production primaire dans les récifs coralliens. Annales de L'Institut Océanographique 53:47–74.

SPENCER, C. P. 1975. The micronutrient elements. Pages 245–300 *in* J. P. Riley and G. Skirrow, eds. Chemical Oceanography 2. Academic Press, London.

STEEMAN-NIELSEN, E., and V. K. HANSEN. 1959. Measurements with the carbon-14 technique of the respiration rates in natural populations of phytoplankton. Deep-Sea Res. 5:222–233.

STRICKLAND, J. D. H., and T. R. PARSONS. 1972. A practical handbook of seawater analysis. 2d ed. Bull. Fish. Res. Bd. Can., 167. 310 pp.

SUNN, LOW, TOM and HARA, INC. 1976. Kaneohe Bay urban water resources data evaluation study. Prepared for U.S. Army Engineer District, Honolulu. 7 separately numbered chapters + 2 appendices.

SZYPER, J. P., J. HIROTA, J. CAPERON, and D. A. ZIEMANN. 1976. Nutrient regeneration by the larger net zooplankton in the southern basin of Kaneohe Bay, Oahu, Hawaiian Islands. Pac. Sci. 30:363–372.

TAGUCHI, S. 1980. Sedimentation in Kaneohe Bay, Oahu, Hawaii 1977 and 1978. University of Hawaii, Hawaii Inst. Mar. Biol. Tech. Rep. 36. 160 pp.

TAKASAKI, K. J., G. T. HIROSHIMA, and E. R. LUBKE. 1969. Water resources of windward Oahu, Hawaii. U.S. Geol. Surv. Water Supply Paper 1894. 119 pp.

TALBOT, F. H. 1965. A description of the coral structure of Tuita Reef (Tanganyika Territory, East Africa), and its fish fauna. Proc. Zool. Soc. Lond. 145:431–470.

TALBOT, F. H., and B. GOLDMAN. 1972. A preliminary report on the diversity and feeding relationships of the reef fishes of One Tree Island, Great Barrier Reef System. Pages 425–442 *in* Proc. 1st Internat. Symp. Corals and Coral Reefs. Vol. 1. Marine Biological Association of India, Cochin.

TESTER, A. L. 1951. The distribution of eggs and larvae of the anchovy, *Stolephorus purpureus* Fowler in Kaneohe Bay, with a consideration of the sampling problem. Pac. Sci. 5:321–346.

U.S. DEPARTMENT OF COMMERCE. (issued annually). Tide Tables, Central and Western Pacific Ocean and Indian Ocean.

———. (issued annually). U.S. Geological Survey, water-data reports, 1960–1979.

VINOGRADOV, A. P. 1953. The elementary composition of marine organisms. Mem. II., Sears Found. Mar. Res., New Haven. 647 pp.

WEBB, K. L., and L. W. HAAS. 1976. The significance of urea for phytoplankton nutrition in the York River, Virginia. Pages 90–102 *in* M. Wiley, ed. Estuarine processes 1. Academic Press, New York.

WEBB, K. L., W. D. DUPAUL, W. WIEBE, W. SOTTILE, and R. E. JOHANNES. 1975. Enewetak (Eniwetok) Atoll: aspects of the nitrogen cycle on a coral reef. Limnol. Oceanogr. 20:198–210.

WEISS, R. F. 1970. The solubility of nitrogen, oxygen, and argon in water and seawater. Deep-Sea Res. 17:721–735.

WHITE, J. K. F. 1980. Distribution, recruitment, and development of the borer community on shallow Hawaiian reefs. Ph.D. Thesis. University of Hawaii, Honolulu. 223 pp.

WIEBE, W. J. 1976. Nitrogen cycle on a coral reef. Micronesica 12:23–26.

———. 1979. Anaerobic benthic microbial processes: changes from the estuary to the continental shelf. Pages 469–485 *in* R. J. Livingston, ed. Ecological processes in coastal and marine systems. Plenum, New York.

WIEBE, W. J., R. E. JOHANNES, and K. L. WEBB. 1975. Nitrogen fixation in a coral reef community. Sci. 188:257–259.

WINER, B. J. 1971. Statistical principles in experimental design. 2d ed. McGraw-Hill, New York. 907 pp.

YOSHIHARA, T., and P. C. EKERN. 1978. Assessment of the potential of solar energy in Hawaii, final report. University of Hawaii, Hawaii Natural Energy Inst. 49 pp. + appendices.

YOUNG, R. H. F., L. S. LAU, S. K. KONNO, and H. H. LEE. 1976. Water quality monitoring: Kaneohe Bay and selected watersheds, July to December 1975. University of Hawaii, Water Resources Research Center Tech. Rep. 98. 87 pp.

YOUNG, R. H. F., K. L. MURPHEW, and N. C. BURBANK, JR. 1973. Water quality. University of Hawaii, Water Resources Research Center Tech. Rep. 31:267–323.

APPENDIX
STANDARD FIELD AND LABORATORY METHODS

GENERAL FIELD WATER SAMPLING

Samples were taken from outboard boats at each of the sampling stations approximately twice a month, except that during the diversion period the sampling frequency at the OF and SE stations was increased. Because of logistical problems, the sampling dates for the chemistry, phytoplankton, and zooplankton teams did not normally coin-

cide. Samples from all four stations were taken within a five-hour period by each sampling team.

CHEMICAL ANALYSIS

Field Measurements

The variables measured in situ included (1) salinity ($\pm$ 0.1‰), (2) temperature ($\pm$ 0.1°C), (3) dissolved oxygen ($\pm$ 0.1 $mg \cdot l^{-1}$), and (4) light transmission ($\pm$ 5%). Complete water-column profiles of these variables were recorded at each sampling site at depths of 1, 2, 3, 4, 6, 8, 10, and 12 m (only to 6 m at the OF station). Salinity and temperature measurements were taken with a Beckman model RS5-3 portable salinometer. The dissolved oxygen concentrations were measured with a YSI model 57 dissolved oxygen meter. The oxygen probe was calibrated in a small jar of air-equilibrated surface seawater according to standard procedures supplied with the instrument. Water clarity (light transmissibility) at each site was measured with a Hydroproducts model 612S transmissometer with a 1-m path length.

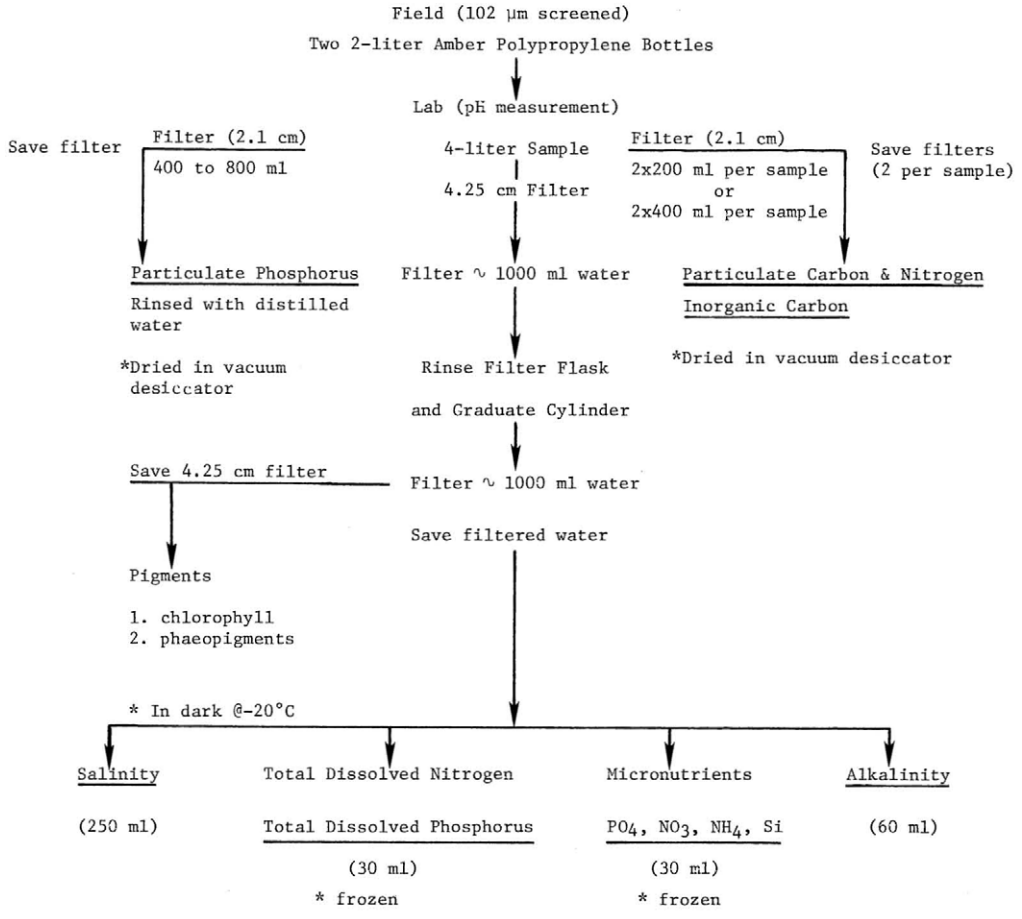
Field Sample Collection and Processing

Procedures for field collection and screening of the seawater samples are listed in the phytoplankton methods section. Two 2-liter samples were returned to the lab and processed within four hours according to the general flow chart shown in Figure 50. Following pH measurement, each sample was divided into three filtering setups. Duplicate aliquots of 200 or 400 ml were collected on precombusted GFC (2.1-cm) filters for particulate carbon and nitrogen determinations. Aliquots of 400 to 800 ml were collected on 2.1-cm filters for particulate phosphorus determinations. One or 2-liter aliquots were collected on 4.25-cm GFC filters for pigment analysis; half of the filtered water was used to rinse all the filtering apparatus to minimize contamination. The second half of the pigment filtrate was divided into sample bottles for salinity, alkalinity, and nutrient analyses. Samples for dissolved organic carbon measurements were collected and processed independently of the other samples. The DOC samples were collected and processed in Chromerge®-cleaned glassware to minimize contamination from plastics. Total processing time for a set of 12 bay samples (see Phytoplankton Methods) was typically less than 4 hours.

Laboratory Methods

Seawater sample salinity values were calculated from conductivity measurements obtained on a Plessey-Grundy model 6230N laboratory salinometer. Primary calibration of the salinometer was performed every few months against Standard Copenhagen Seawater of known chlorinity. Daily secondary calibration was checked against a substandard of filtered open-ocean water poisoned with mercuric chloride, and stored in a tightly stoppered glass jug. During sample measurements, the substandard was run as an unknown every ten samples to account for drift from the initial standardization setting at the beginning of the day. A salinity sample of 250 ml was enough to rinse the sample bowl and obtain triplicate conductivity measurements. Typical bay waters had salinities in the range of 32 to 35‰. Reproducibility of the salinity analyses was less than $\pm$ 0.005‰.

The methods used for measuring and calculating pH and alkalinity are described by Smith and Kinsey (1978). These procedures are slightly modified versions of the standard methods listed by Strickland and Parsons (1972). Field measurements of pH and temperature were obtained with a digital voltmeter ($\pm$ 0.1 mV) equipped with a thermistor and a Sensorex combination electrode. Commercially available buffers of pH 7.02 and 4.00 were used daily for calibration and electrode slope adjustments. A secondary seawater "Tris" buffer was used internally to account for drifts during the measurement period. Daily precision was within $\pm$ 0.003 pH units; however, pH readings are considered accurate to only $\pm$ 0.02 pH units because of occasional erratic shifts



Notes: 1. *Storage conditions prior to analysis
2. All filters precombusted (500°C, 4 hrs) GFC grade
3. All glassware and sample bottles were prerinsed with 10% HCl, distilled water and sample water

FIGURE 50. Flow chart for water chemistry sample processing.

in electrode response. Total alkalinity of the seawater samples was measured with a Corning model 101 digital pH meter using a Sensorex combination electrode. The calibration procedure was identical to that for pH readings except that the calibrated electrode was soaked in a "dummy" alkalinity sample for 1 hour to stabilize the electrode prior to sample measurements. The alkalinities of most bay waters were between 2.2 and 2.4 meq·l^{-1}. Daily precision within a given set of analyses was better than $\pm$ 0.004 meq·l^{-1}. Total CO_2 was calculated from pH, total alkalinity, temperature, and salinity.

Filtered seawater samples for dissolved organic carbon analyses were measured on a model 0524B Total Carbon Analyzer (Oceanography International Corp.). The procedure involved four basic steps: (1) filling precombusted glass ampules with 10 ml of sample water, 0.25 ml of 6 percent H_3PO_4, and 0.2 g of $K_2S_2O_8$; (2) purging the ampules of inorganic carbon using purified oxygen (passed through cupric oxide at 475° C) and sealing; (3) oxidizing dissolved

organic carbon to CO_2 by autoclaving the ampules at 130° C for 4 hours; and (4) measuring the concentration of CO_2 released inside the ampule using a nondispersive infrared analyzer. Calibration curves were obtained daily by direct injection of a given range of volumes of a standard solution of Na_2CO_3 (0.4 $\mu gC \cdot \mu l^{-1}$). The Na_2CO_3 curves were cross-checked periodically against organic standards (glucose, sucrose). Standard error on duplicate analyses was found to be less than $\pm$ 0.2 mg $C \cdot l^{-1}$, or about 10 percent of the concentration.

Methods for chlorophyll pigments and carbon and nitrogen analyses of particulate material collected on precombusted GFC filters are listed in the Phytoplankton Methods section. Carbon and nitrogen determinations of sediment materials were also performed on a Hewlett Packard 185B CHN analyzer. Organic and inorganic carbon concentrations were determined by the technique described by Hirota and Szyper (1975), in which the ground, dried sediment was analyzed before and after ashing at 500° C for 4 hours. Precision standard errors on duplicate analyses were $\pm$ 0.5 percent ash, $\pm$ 0.2 percent carbon (inorganic and total), and $\pm$ 0.05 percent nitrogen.

The method for particulate phosphorus determinations was developed during the course of this study, and used successfully on cultured phytoplankton collected on precombusted GFC filters, individual fresh zooplankton, dried zooplankton ground up with its accompanying filter, dried and ground benthic algae, and sediments (J. Szyper, unpublished data). The procedure involved four steps:

1. Addition of 1.0 ml of concentrated H_2SO_4 to the test material ($\sim$ 20 mg of ground solids or 400–800 ml of aliquots of seawater collected on GFC) at the bottom of a 50-ml graduated glass digestion tube and incubation in a boiling water bath for one hour.

2. Dilution to $\sim$ 25 ml with distilled water and reheating in the water bath for 30 minutes to hydrolyze polyphosphates (Strickland and Parsons 1972).

3. Partial neutralization with 5.0 ml of 5N NaOH, final dilution to 35.0 ml with distilled water, mixing using a vortex mixer. The product waters were then filtered through precombusted glass filters.

4. Analysis of the product waters for orthophosphate as described below.

Typical product water for most ground solids yielded at least 20 μM PO_4 with blanks of $\sim$ 0.3 μM PO_4. Product water for most bay-water particulates collected on filters was about 1 to 3 μM PO_4, with blanks of $\sim$ 0.3 μM PO_4. Precision standard errors on duplicate analyses were approximately $\pm$ 0.002 percent P for ground solids and $\pm$ 0.3 $\mu mole\ P \cdot l^{-1}$ for bay-water particulate material.

Micronutrient concentrations of seawater samples were determined according to somewhat modified versions of the methods listed by Strickland and Parsons (1972). The analyses were performed on a Technicon Autoanalyzer II system. Additional detailed information on these methods can be obtained by request (Technicon Industrial Systems, Tarrytown, New York 10591; Industrial Methods for Water, Seawater and Wastewater Analysis). A brief description of the method for each type of nutrient analysis is in order.

$PO_4^{\equiv}$ (as orthophosphate) was determined by the addition of an acidified solution of ammonium molybdate containing ascorbic acid and a little antimony. A blue phosphomolybdenum complex was formed and read colorimetrically at 880 nm (Murphy and Riley 1962). A working standard of 4.0 $\mu mole \cdot l^{-1}$ was prepared fresh daily by dilution of a stock standard of 500 $\mu mole \cdot l^{-1}$ KH_2PO_4. The method was linear up to 50 μM with a precision standard error on duplicate analyses of approximately $\pm$ 0.05 $\mu mole \cdot l^{-1}$ or 5 percent of the concentration (whichever was greater).

The $NO_2^- + NO_3^-$ method had three steps: (1) reduction of nitrate to nitrite using a copper-cadmium reduction column, (2) reaction of nitrite with sulfanilamide forming a diazo compound under acidic conditions, and (3) coupling of the diazo compound

with N–1 napthylethylenediamine dihydrochloride, which forms a purple azo dye. The resulting dye concentration, which is proportional to the nitrate + nitrite concentration, was read colorimetrically at 550 nm (Armstrong, Williams, and Strickland 1966). A working standard of 5.0 $\mu mole \cdot l^{-1}$ was prepared fresh daily by dilution of a stock standard of 2500 $\mu mole \cdot l^{-1}$ KNO_3. The method was linear up to 200 μM, with a precision standard error on duplicate analyses of approximately $\pm$ 0.05 $\mu mole \cdot l^{-1}$ or 5 percent of the measured value.

The NH_4^+ procedure involved addition of sodium phenoxide and sodium hypochlorite to the sample stream; this forms a blue-colored ammonium complex. Interfering hydroxides of calcium and magnesium were eliminated by adding potassium sodium tartrate and sodium citrate to prevent precipitation. The resulting color reactions were measured at a wavelength of 630 nm. A working standard of 5.0 $\mu mole \cdot l^{-1}$ was prepared fresh daily from a stock standard of 500 $\mu mole \cdot l^{-1}$ $(NH_4)_2SO_4$. The method was linear up to 50 μM. Precision standard error on duplicate analyses was approximately $\pm$ 0.2 $\mu mole \cdot l^{-1}$, or 10 percent of the measured value.

The automated Si procedure (somewhat modified from Strickland and Parsons 1972) for determining reactive soluble silicates in seawater consisted of three steps: (1) introduction of oxalic acid to eliminate interfering phosphates, (2) formation of a silicomolybdate compound, which is (3) reduced to a molybdenum blue complex under acidic conditions by ascorbic acid. The complex obtained was read colorimetrically at 660 nm. A working standard of 10 $\mu mole \cdot l^{-1}$ was prepared fresh daily from a stock standard of 5000 $\mu mole \cdot l^{-1}$ Na_2SiF_6. The method was linear to about 400 μM, with a precision standard error on duplicate analyses of approximately $\pm$ 0.5 $\mu mole \cdot l^{-1}$, or 10 percent of the measured concentration.

The method used for total dissolved phosphorus and nitrogen involved initial digestion of total dissolved N and P in a filtered seawater sample followed by autoanalyzer colorimetric analysis of the digestion products (soluble orthophosphate and nitrite; Strickland and Parsons 1972). The digestion technique (Armstrong, Williams, and Strickland 1966) involved: (1) adding 2 to 3 drops of 30 percent H_2O_2 to a clean silicate 30-ml test tube containing filtered seawater, (2) ultraviolet irradiation for 3 to 4 hours, (3) cooling to room temperature, and (4) analysis for orthophosphate and nitrite + nitrate. The ultraviolet irradiation in the presence of excess oxygen oxidizes all phosphorus to the soluble orthophosphate; most nitrogen is converted to inorganic nitrogen. NH_4 and $NO_3 + NO_2$ are analyzed by standard automated procedures to yield total dissolved nitrogen. Precision standard error on duplicate analyses was approximately $\pm$ 0.05 $\mu mole \cdot l^{-1}$ or 5 percent for total dissolved phosphorus and $\pm$ 0.3 $\mu mole \cdot l^{-1}$ or 10 percent for total dissolved nitrogen.

PHYTOPLANKTON ANALYSES

Field Sampling

Water samples were taken using a modified bilge pump fitted with a garden hose. Primary production measurements on water samples taken before and after passing through the pump were found not to be significantly different (t test, $p < 0.05$). The water from the pump was screened through 102-μm-mesh nylon gauze in order to remove the larger zooplankton. Samples were taken from depths of 1 m, 5 m, and 10 m at the NW, CE, and SE stations, and from 1 m, 3 m, and 5 m at the shallower OF station.

Laboratory Methods

Water samples to be analyzed for nutrients and particulate concentrations were stored in polyethylene bottles which had been acid-cleaned and rinsed with distilled water. These samples were stored in the dark at ambient water temperature until they were filtered. Filtering was generally completed within 4 to 5 hours of the collection

time. Samples for particulate carbon and particulate nitrogen analysis were processed as discussed in the chemical analysis section.

Two-liter samples for chlorophyll analysis were filtered onto GFC filters and analyzed following the procedures recommended by Jeffrey (1974) and Jeffrey and Humphrey (1975). Phaeopigment corrections were made following the procedures in Strickland and Parsons (1972).

For ATP extractions, either 200- or 400-ml samples were filtered onto Nuclepore 0.4 micron polycarbonate filters; the particulate ATP was extracted in boiling Tris buffer at a pH of 7.7. The ATP was assayed with an AMINCO photometer by the procedure of Holm-Hansen and Booth (1966), but employing the luciferase enzyme preparation of Karl and La Rock (1975). Initially the assay was performed by the integration method (Holm-Hansen and Booth 1966), but after June 1977, the peak-height method was employed. This change in procedure resulted from the discovery that the integration method fails to distinguish between ATP and other nucleotide triphosphates, particularly GTP, and hence may seriously overestimate the amount of ATP in a sample (Karl 1978). Comparison of ATP results before and after this change in method indicated that the integration method overestimated ATP concentrations by about 50 percent at the NW, CE, and SE stations, and by about 20 percent at the OF station.

Samples for nutrient analysis were treated as discussed in the chemical analysis section.

Primary production measurements were made using ^{14}C according to the basic procedures in Strickland and Parsons (1972), except that 60 ml BOD bottles were used to incubate the samples and the assimilated ^{14}C radioactivity was determined by counting on a Searle Analytic Delta 300 liquid scintillation counter. The activity of ^{14}C spikes was determined following the recommendations of Iverson, Bittaker, and Meyers (1976). The BOD bottles were incubated in situ between approximately 0930 and 1230 hours. On three occasions, sunrise-to-sunset incubations were done in conjunction with short-term incubations to determine the relationship between daily and short-term (i.e., 0930–1230 hr) production.

ZOOPLANKTON ANALYSES

Field Sampling

At each station the bottom was sounded with a sounding lead, and a Secchi disk reading was taken. Surface water samples were taken on some occasions for particle counts.

At each station duplicate vertical plankton tows and a single surface (neuston) tow were taken. At one of the four stations on each date an additional neuston tow was also taken. A double frame sampler (described by Clutter 1973; similar to a bongo net) was used for the vertical hauls. This sampler consists of a rigid aluminum frame with a central tow point and two rings, to which are attached two nets. One net is a 0.5 m, 333-μm-mesh conical net for macroplankton, the other a double net with a 35-μm outer mesh for microplankton and a 333-μm inner mesh for prescreening, and a 35-cm mouth diameter reducing cone. The cod ends of the nets were clamped into a weighted aluminum bracket suspended from the frame just below the tow point to prevent the nets from fouling during descent. Both nets were equipped with TSK flowmeters, one of which was stopped with string to prevent turning; the string was pulled free just before the haul.

The vertical sampler was lowered and raised with a gasoline-powered winch and a davit. The sampler was lowered to 1.5 m off the bottom, at which point the weight rested on the bottom. After the flowmeter blades had been freed, the sampler was hauled, at a speed of about 75 $cm \cdot sec^{-1}$, to the surface. The catch of the 35-μm and single 333-μm nets only were retained; the catch of the inner 333-μm net was discarded after each pair of hauls. Flowmeter readings from the stoppered flowmeter were used to establish net efficiency, which was 100 percent for the 333-μm net and 70 percent for the 35-μm net. Differences in 35-μm net efficiency

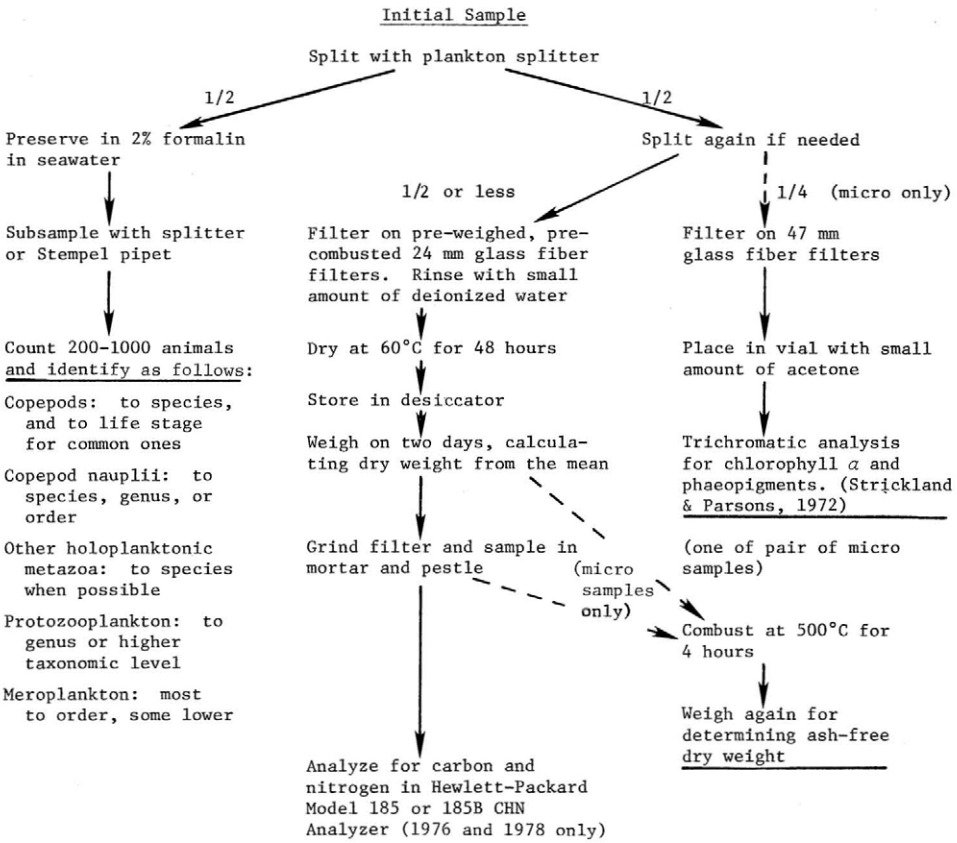


FIGURE 51. Flow chart for zooplankton sample processing.

among stations, while significant, were small and were therefore neglected. Volumes filtered were calculated from net efficiency and depth of tow.

Neuston samples were taken with a 333-μm-mesh, 0.5-m diameter net equipped with a flowmeter and towed so that the upper edge of the net broke the surface. Towing speed was about 1.5 $m \cdot sec^{-1}$, and duration was 0.5 to 5 minutes. The boat was driven in a circular path to keep the net free of the boat's wake.

After each tow, nets were rinsed from the outside with surface seawater from a battery-powered bilge pump to concentrate samples in the cod ends. Samples were poured into plastic jars and placed on ice for transport to the laboratory. The time between sampling and processing was kept under three hours to minimize loss of body contents by the animals.

Laboratory Methods

Figure 51 shows how zooplankton samples were processed. Surface water samples were processed with a Coulter Counter model TA-II with a 70-μm orifice using the 0.5-cc manometer mode.

BENTHOS ANALYSES

Field Sampling

A fringing reef station consisted of a permanent transect running from the shoreline across the reef flat over the reef crest and

down the forereef slope to the muddy lagoon floor. The patch reef transect was identical but began on the reef flat adjacent to the reef crest due to its being offshore. The transects were marked every 20 m by a permanent steel stake. During each sampling period, a 200-m transect line was laid down, following the stakes, to locate specific sampling sites.

Benthic sampling was carried out on an approximate bimonthly schedule. During each sampling period, a number of different sample types were taken at specific sites including a visual appraisal of resident fish populations, infaunal samples (both hard and soft substratum) for estimation of standing crop, benthic macroalgal biomass samples, substratum samples for chemical analysis and grainsize distribution, macroalgal samples for epifaunal analysis, and quadrats to estimate the species composition and cover of benthic organisms (corals, other macroinvertebrate species, algae, and inanimate substratum). Once every six months, the hard and soft substratum infaunal samples were used to determine the species composition.

Data were accumulated through both destructive and nondestructive techniques. The nondestructive methods included visual fish transects and quadrat estimates of large sessile benthic components. These techniques allowed one to resample the same area over time. Removal of substratum as in the infaunal studies or algae for standing crop analysis created a localized disturbance and precluded application to precisely the same location more than once; rather, through careful measurement, samples were taken within 15–40 cm of one another at a given locality over the four-year program.

Visual fish censuses were conducted according to a modification of the technique of Brock (1954). A diver noted the abundance of all fish species seen within 4 m of a 20-m transect line. Fish censuses were conducted at all stations on the lagoon floor, the forereef slope, the reef crest, and at several locations on the shallow reef flat.

Percent cover by large sessile benthic organisms was assessed by use of a 1×1-m frame subdivided into 10×10-cm squares. The frame was located exactly by use of permanent stakes.

Where macrothalloid algae were abundant enough to be readily harvested (i.e., greater than 1 to 2 $g \cdot m^{-2}$ dry weight), a 0.1-m^2 ring was used in sampling. The ring was placed at specific locations (within 50 cm of previous sampling points); all algae within the ring were removed, bagged, labeled, and frozen for later analysis. Algal epifauna samples were collected in the same manner but were fixed in 10 percent buffered formalin.

Soft substratum samples were collected in all physiographic zones (lagoon floor, forereef slope, reef crest, and reef flat) at every station where sufficient material occurred. However, following initial analysis it became apparent that the soft-bottom communities of the forereef, reef crest, and flat biotopes were very similar. Therefore sampling of the soft bottom infauna was restricted to the lagoon floor and the reef flat areas. Samples were collected by pushing a 30-cm-high stainless steel cylinder (0.2 m^2 cross-sectional surface area) approximately 15 cm into the substratum. The sediment within the cylinder was quickly scooped out to a 10-cm depth into 0.5-mm-mesh bags, labeled, tied, and fixed in 10 percent buffered formalin. The use of mesh bags allowed for a quick washing through of small particles and rapid fixing of specimens. In the laboratory these samples were used in biomass analysis or for the determination of species composition of the community.

Hard substratum samples were removed by use of a mason's hammer. The size of the sample varied, but hard material (usually dead coral) was taken such that it approximated 100 cm^2 in exposed surface area and was removed to a depth of 10 cm. These samples were subjectively selected as to their being representative of the habitat and for ease of removal. Samples were either broken free and immediately placed in plastic bags or a bag was placed over a projecting piece of substratum that was subsequently broken loose. All samples were labeled and preserved in 10 percent buffered formalin until laboratory analysis for standing crop or species composition.

During each field sampling period, sediment samples were collected for chemical and grain size analyses. Samples were taken

with a 1-liter plastic scoop, placed in new plastic bags, tagged, and frozen until later laboratory analysis.

Laboratory Methods

Algal biomass samples were sorted to species and oven-dried at 60° C to a constant weight. Standing crop values were calculated in $g \cdot m^{-2}$ dry weight. Algae collected for epifaunal analyses were rinsed over a 0.5-mm screen to catch epifaunal organisms. These samples were subsequently oven-dried to constant weight at 100° C.

Infaunal sediment samples were gently rinsed in their mesh bags to remove fine particulate material. The displacement volume of the material remaining was measured; the material was subjected to an acidification process to remove calcium carbonate (Brock and Brock 1977), leaving detritus and organisms behind. The settled volume of this material was determined, and organisms were sorted from the detritus and oven-dried at 100° C for standing crop estimates or sorted to various taxa for species composition studies. All standing crop estimates were calculated on a $g \cdot m^{-2}$ dry weight basis.

Volume displacement, wet weight, and rough linear measurements of the exposed surface (for area determinations) were made on hard substratum samples. After acid dissolution (Brock and Brock 1977) the total settled volume of material remaining was measured and organisms were sorted from the matrix of material. These were either dried at 100° C for biomass estimates or sorted to a number of taxonomic levels for information on community structure.

In all infaunal (sedimentary) and cryptofaunal (endolithic) laboratory work, the screen and mesh size used was 0.5 mm. Thus, organisms smaller than 0.5 mm in some dimension (the meiofauna) could pass through and be lost from further analysis.

The 1-liter sediment samples taken for chemical and grain size analyses were thawed, and a 50-g subsample was taken and oven-dried for later determinations of percent ash, total carbon, inorganic and organic carbon, as well as total nitrogen. Approximately 500 g of the material was used in the analysis of grain size and the remainder was discarded.

To analyze the distribution of grain sizes in a sediment sample, a set of Tyler Standard (8.5-inch diameter) geological screens in a graded series from −4 to 4 phi (ϕ) units (i.e., mesh openings of 16, 8, 4, 2, 1, 0.5, 0.25, 0.125, 0.063, < 0.063 mm) were used. Samples of about 105 to 200 ml in volume were wet sieved through the series of screens. The size fractions were dried at 100° C to constant weight, weighed, and the weight of each size fraction was calculated as a weight percent of the total sample. These values were plotted on probability paper as cumulative weight percent against particle size in phi (ϕ) units.

Sediment samples were prepared for CHN analysis by drying them in crucibles at 80° C for several days, and analyzed according to the technique described in the Chemical Analysis section.

ENVIRONMENTAL VARIABILITY

Some of the variability seen in the water-column data (e.g., chlorophyll and zooplankton biomass) could result from environmental variability unrelated to sewage diversion. To prevent such variability from masking the sewage effect, we analyzed some of these data for correlation with several environmental variables. Specifically, we were interested in the effects of wind speed and direction, light, temperature, rainfall, runoff, and tidal amplitude. All but the last of these can be correlated with each other both seasonally and on a shorter time scale. Rigorous application of multiple regression and covariance analyses requires that independent variables be uncorrelated. We therefore extracted a set of orthogonal (i.e., uncorrelated) predictor variables from the original set.

The raw environmental variables were: daily mean wind speed and direction from a wind gauge at Coconut Island; daily insolation taken from an integrating photometer at Coconut Island; monthly rainfall from a rain gauge at Coconut Island; monthly

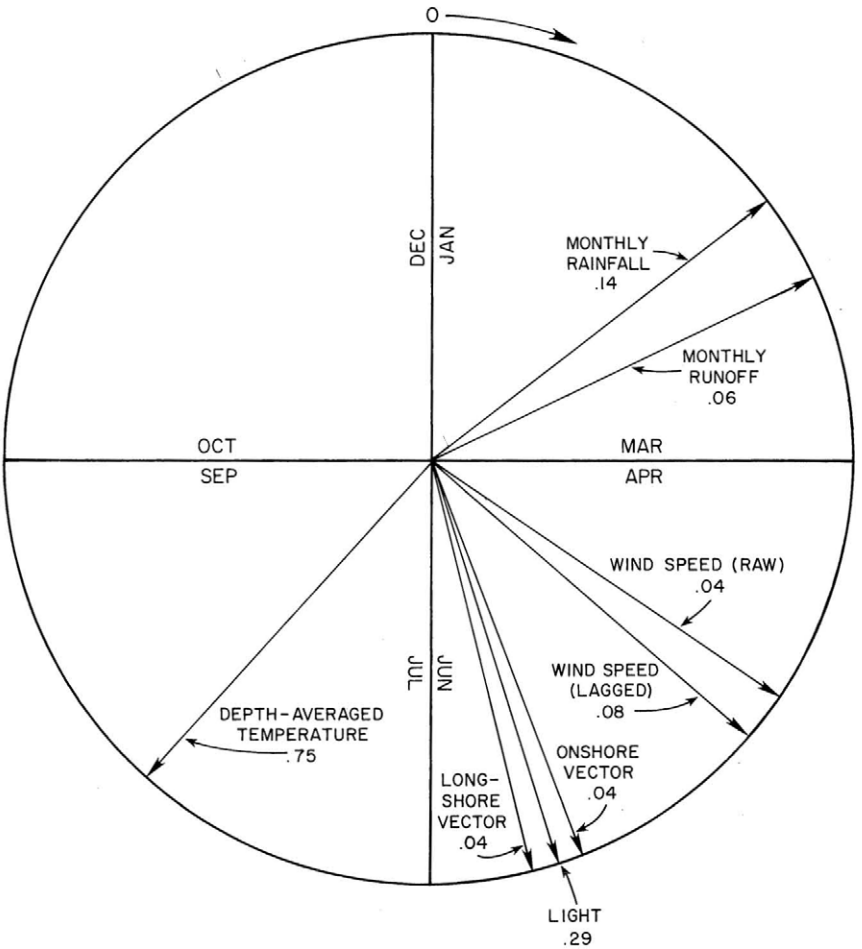


FIGURE 52. Phase angle for maximum values and coefficients of determination for the relationships between an annual sine plus cosine function and major environmental variables.

runoff from a stream gauge on Kamooalii Stream (which is highly correlated with data from other stream gauges); water temperature taken during routine water density sampling; and tidal amplitude from tide prediction charts.

Wind was believed to affect the ecosystem on time scales from hours to weeks, and to vary its effect depending on direction. We therefore decomposed the wind-speed data into vectors perpendicular to and parallel to the long axis of the bay (i.e., 45° and 135°). We also computed long-term smoothed wind speeds using weighting functions which decreased exponentially with increasing lag; these were cut off at 5, 11, and 22 days, at which time they reached 10 percent of their initial values.

The seasonal components of each of the variables except tidal amplitude were removed using a regression against a sine and cosine function with a one-year period. The resulting phase angles and coefficients of determination (Figure 52) show to what extent each variable was seasonal, and how the seasonal cycles are related to each other.

Principal components factor analyses were performed on the residual data to derive additional uncorrelated variables (see Rummel [1967] for a lucid summary of

factor analysis). Rainfall and runoff combine into a single factor, and the various wind speeds are contained in three factors: a long-term factor; a short-term onshore factor; and a short-term long shore factor. Residual light after removal of the seasonal component, largely a function of cloudiness, did not correlate well with the four factors and was thus treated directly as an independent variable, as was tidal amplitude. Water temperature had high seasonal predictability, and its residual is largely contained in the long-term wind factor and residual light variable.

We have thus reduced the original 13 highly correlated environmental variables to index variables that are only weakly correlated but contain most of the statistical information of the original 13. These variables are appropriate for regression and covariance analysis against the dependent variables that describe the ecosystem.

STATISTICAL ANALYSES

Most of the statistical techniques we used are straightforward, and descriptions can be found in any standard text (e.g., Sokal and Rohlf 1969). Two exceptions are mentioned below. One is the use of analysis of covariance with repeated measures (Winer 1971) on some of the chemistry and zooplankton data. In this method the data from four stations are treated as repeated measures of a single variable under four treatments. This permits us to discern differences among stations that might otherwise be masked by temporal variability affecting all of the stations.

The second exception concerns regression analysis. The regression analyses reported here examined the relationship between two variables, both of which had been measured with error. Normal regression techniques are appropriate only if the independent variable has small or zero error in measurement. For the cases where this assumption could not be met, we used a geometric mean regression (Ricker 1973), in which the result does not depend on the choice of which variable is used as the independent variable and which is the dependent variable.